LIVING CHAMIDAE OF THE EASTERN PACIFIC (BIVALVIA: HETERODONTA)[1]

By F. R. Bernard[2]

Abstract: Nineteen species of Chamidae live in the American Eastern Pacific and occur predominantly in shallow warm waters. The extensive collections of the Allan Hancock Foundation, University of Southern California, provided the basis for this distributional and systematic review. It is concluded that the valve of attachment is genetically determined. A reinterpretation of hinge ontogeny is presented. *Pseudochama dalli* nom. nov. is proposed for a preoccupied name. Three new species, *Chama arcana, C. garthi,* and *C. tinctoria* are proposed.

INTRODUCTION

The Superfamily Chamacea is represented by the single family Chamidae, comprising epithetic (attached) dimyarian bivalves inhabiting shallow tropical to temperate waters. Maximum abundance is just sublittoral, though a few species have been collected down to 200 meters; deep records such as 2300 meters (Locard 1898) for *Chama nicoloni* Dautzenberg, 1892 are probably attributable to transported material (Clarke 1962). The largest and most diverse faunule is Indo-Pacific. Approximately 70 living species are represented world-wide of which 19 are eastern Pacific.

The amount of chamid literature is small and scattered. The modern comprehensive taxonomic treatment is that by Lamy (1927), while anatomical and systematic reviews by Odhner (1919) and Yonge (1967) reached somewhat contradictory conclusions. Bayer (1943) reviewed some Caribbean species. In the course of preparing a world-wide survey of the family, the large holdings of the British Museum (Natural History), the Paris Museum, the Stockholm Rijksmuseet, and the United States National Museum, were studied and compared, as well as material in the California Academy of Sciences, Los Angeles County Museum of Natural History, and the S. S. Berry collection. This paper is based upon the important West American collections made since 1931 by the Allan Hancock Foundation and its predecessor, the Hancock Pacific Expeditions, which have yielded new distributional records, three new species, and a sufficient series of juvenile specimens to clarify probable hinge ontogeny.

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Chamids are generally highly inequivalve, with strongly prosogyrate beaks. During development the beaks become separated, resulting in the longitudinal splitting of the substantial parivincular ligament. The external shell surface may be ornamented with regular lamellae or spines or may be entirely smooth, particularly in gerontic specimens. Cup-shaped outgrowths analogous to the hyote spines of some Indo-Pacific pycnodontid oysters are usually present on the cemented valve and probably serve as supports for sensory folds of mantle tissue (Rudwick 1965). The commissural outline is usually rounded but may be elongate, particularly in *Pseudochama*. In nearly all species the commissure margins display a flattened area set off at an obtuse angle from the general curve of the internal shell surface. This region is analogous to the commissural shelf of some oysters and consists of the outer and middle shell layers only, and may be crenulated or nodulose.

Chamids are either permanently cemented to the substrate or undergo a brief phase of attachment during development. In all genera the unattached valve carries a single laterally elongated tooth-like process that fits into a socket in the attached valve. While the juvenile dentition displays a generalized heterodont pattern, adult dentition is entirely different. Attempts to homologize the mature configuration to early dissoconch hinge structures have led to unsatisfactory conclusions and inability to resolve the systematic significance of the valve of attachment.

All the permanently attached chamids are strongly inequivalve, the free valve often being little more than a discoid operculum closing off the large cup-shaped attached valve. This group is extremely xenomorphic, moulding to the substrate and losing most external characters such as spines in mature specimens. The noncemented genus *Arcinella* displays a well-developed lunule that is absent in other taxa, but some attached chamids have a trace of an obscure escutcheon on the free valve. In all groups the ligament is external, but may be deeply sunk and overgrown by the outer shell layers.

Chamids are stenohaline nearshore inhabitants of rocky shores and coral reef communities. Their poor ability to withstand lowered salinity prevented their colonization of estuarine regions. Their distribution is limited to areas with little sedimentation, and habitats fall into two major categories. The greater number of species are cemented to massive rocks in exposed areas, from the mid-tidal zone to a few meters depth. These individuals are large, thick-shelled and bear little shell ornamentation. The other group comprises the smaller, thin shelled species with small areas of attachment and pronounced shell ornamentation. These individuals live as nestling epifauna, frequenting fissures and crannies, as well as the underside of boulders. This group has a wider bathymetric range than the first, frequently occurring in 20 or more meters, cemented to small pebbles, shells, or coral.

It is now well established that chamids and the extinct rudists had no common phylogenetic links, yet the distribution and ecological niche of the two taxa is strikingly similar. Dacqué (1915) noted the low latitude circumglobal distribution of rudists, an observation strengthened by Hamilton's (1956) discovery of rudists dredged from Cape Johnson guyot in the mid-Pacific.

Despite their wide tropical and subtropical distribution, chamids remained conservative in habitat selection, no representatives have been reported in such niches as mangrove roots or floating debris so successfully colonized by other cemented forms. The only experiment appears to be the pseudochamid-descended genus *Arcinella,* which adopted a free existence when adult. It is doubtful if this may be considered a true adaptation, as detachment is purely mechanical, the result of the initial small attachment zone. However, the nearly equivalve condition and the great development of the shell spines are probably contributive to successful free epiphetic existence. The experiment cannot be considered an unqualified success as *Arcinella* is very limited in distribution and is of rare occurrence.

ANATOMY

The gross morphology of the Chamidae is well known from the work by Grieser (1913), the comparative studies by Odhner (1919), and the functional interpretation of Yonge (1967). Only a brief summary is given here based upon observation of preserved *Chama squamuligera* Pilsbry and Lowe; *Pseudochama corrugata* (Broderip), and a single specimen of *Arcinella californica* (Dall).

Chamid soft parts, with the exception of *Arcinella,* are bilaterally asymmetrical, being hypertrophied on the side of attachment; the mantle, ctenidia, gonad and digestive diverticula are enlarged, though the balance of the alimentary, circulatory, and nervous systems are not affected. The ventral migration of the adult functional hinge results in the formation of a deep umbonal cavity, occupied by a prolongation of the mantle, gonad, and connective tissues, similar to that of some Ostreacea. The nature of this body asymmetry has been fully discussed by Yonge (1967).

The mantle is thin, with small marginal folds. Fusion is extensive but involves only the inner fold, except for the dorsal portions, where both the inner and middle folds are fused. The fused border is outside the hinge line and lies just below the ligament, so that an extensive epithelial sheet separates the opposing hinge elements. This interdental epithelium is fenestrated, the openings conforming to the protuberances on the teeth, which are analogous to vermiculate chomata (Stenzel 1971). The presence of a nacre-secreting mantle edge outside the hinge teeth is the main factor leading to the formation of an annular free valve with progressive centralization of the hinge teeth.

The fused mantle borders are furnished with irregularly distributed small tentacles, which are longest in *Arcinella.* Two small thin papillated siphons arise just below the posterior adductor muscle, while the pedal opening occupies most of the anterior face of the anterior adductor muscle. In *Arcinella* the pedal opening is smaller and more ventrally situated, the siphons larger and more muscular. The large adductor muscles are subequal and dorsoventrally elongated. The foot in *Chama* and *Pseudochama* is virtually vestigial and probably not functional. In *Arcinella* it is vermiform and capable of protrusion through the pedal opening.

Chamid ctenidial structure has been exhaustively covered by Menegaux (1890), Ridewood (1903), Grieser (1913), Odhner (1919) and others. This organ is remarkably uniform in all three genera, and consists of two complete demibranchs, the inner one larger than the outer. The lamellae are plicated, synaptorhabdic, with both interfilamentar and interlamellar junctions as well as intraplicatural fusions involving the distal ends of opposing filaments (Ridewood 1903). Ctenidial ciliation falls under "Type C" of Atkins (1937), and Yonge (1967) has dealt with ciliary currents.

The labial palpi are asymmetrically placed and small in *Chama* and *Pseudochama,* and much larger in *Arcinella.* The mouth is wide and overhung by protruding lips. The rest of the alimentary canal is similar in all taxa. A slender plicated oesophagus enters the anterior portion of the stomach, separated from the stomach main chamber by a conspicuous ventral ridge. Crystalline style-pouch and midgut are conjoined. The minor typhlosole terminates on the stomach's right posterior wall, while the major typhlosole, accompanied by the intestinal groove, curves over the left wall and terminates near the openings of the digestive diverticulae. A small dorsal hood is situated on the anterior left side of the stomach. The ducts of the digestive diverticula number about eight and are clustered into four groups. The gastric shield is small. The chamid stomach falls into "Type IV" of Purchon (1958).

The intestine is short, passes dorsally through the ventricle of the heart, then plunges ventrally along the outer surface of the posterior adductor muscle. The anus is removed from the exhalant siphon, so it is possible that faeces are transported by ciliary currents and discarded via the pedal aperture. Odhner (1919) reported variations in intestinal flexure; however, these are probably attributable to indifferent specimen preservation. The specimens examined for this report all conform to the description of Yonge (1967). Pelseneer (1911) claimed partial reversion of the alimentary canal in *Chama* and *Pseudochama;* however, Odhner (1919) did not support this view and Yonge (1967) showed that "inversion" involved the pallial structures only.

The family is dioecious, the extensive gonads occupying the lateral portions of the body, the umbonal cavity, and the dorsal mantle tissues. The eggs are small, fertilization occurs externally, and the larvae probably undergo a prolonged planktonic development (LaBarbera and Chanley 1971).

CEMENTATION

Cementation is usually associated with the monomyarian condition; living cemented dimyarians consist only of the Chamidae, *Myochama, Dimya* and the freshwater Etheriidae. In the Chamidae cementation occurs late in the dissoconch stage (sometimes termed the post-neanic), individuals being 0.5-5 mm total shell length, depending upon ultimate species size. Subsequent to planktonic development, larvae are mobile and temporarily attach by a single byssal thread (LaBarbera and Chanley 1971). Anthony (1905) believed cementations occurred either anteriorly or by the entire valve surface, resulting in an oblique elongated or rounded adult form. However, examination of large series of recently attached individuals and the report by LaBarbera and Chanley (1971) clearly show that cementation is not pleurothetic but involves the new growth margin and results in the anteroposterior axis being perpendicular to the substrate. A period of rapid idiomorphic growth occurs with a strong tangential component in the attached valve which undergoes a coiling growth. The early stages of cementation are presented diagrammatically in figure 1. The more rapid addition to the attached valve results in the progressive separation of the beaks, so that the dissoconch commissural planes come to lie at right angles to each other. The spatial displacement of the umbones causes the longitudinal splitting of the ligament, a process fully described by Owen (1953) and Yonge (1967).

The size of the cementation area bears a direct relationship to the curvature of the two shell valves. If it is extensive, the shell is highly inequivalve with a flat-

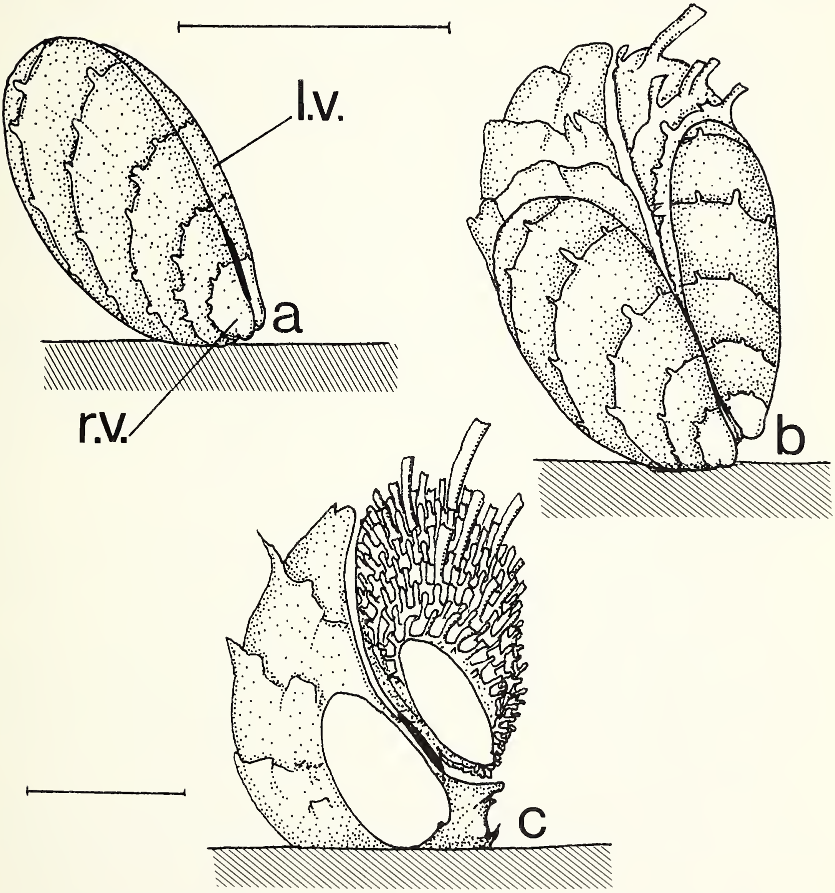

FIGURE 1. Cementation and early growth of *Pseudochama*. (a) Initial attachment; (b) period of rapid idiomorphic growth; (c) assumption of adult form. l.v. = left valve; r.v. = right valve. scale = 1 mm.

tened opercular free valve. Jackson (1890), in a largely overlooked paper, first concluded that mechanical constraints of cementation resulted in a cup-shaped attached valve. Subequivalve chamids such as *C. sordida* Broderip and *C. corallina* Olsson display small cementation zones as does the nearly equivalve genus *Arcinella.*

Lamarck (1819) segregated chamids according to which valve was cemented to the substrate, but Broderip (1835a) failed to distinguish between them, while Reeve (1847) stated that attachment was fortuitous. The systematic significance of left or right valve attachment has not been resolved, though Odhner (1919) divided the permanently cemented Chamidae into two genera. While agreeing that most representatives are consistently attached either by the left or right valve, Lamy (1927) placed all species in *Chama.* Yonge (1967) also rejected the taxonomic significance of attachment, but admitted the convenience of referring to *Chama* and *Pseudochama.*

Which valve is cemented to the substrate is genetically determined and apparent anomalies are nearly all referable to misidentifications. For example the type specimens of the Indo-Pacific *C. pulchella* said by Reeve (1847) to be indifferently attached (Syntypic Series BM(NH) 1950. 11.1 49-51) certainly consists of two species, the smaller individuals, the nominate species; and the larger specimen is *P. similis* Odhner 1917. The attached left and right valves figured by Palmer (1928), said to be *C. pellucida* Broderip, represent typical specimens of this species and of *P. exogyra* (Conrad), whose ranges overlap. Taylor and Kennedy (1969) repeated the observation that *C. pellucida* may sometimes attach by the right valve. I have examined long series of this species without noting a single case of anomalous attachment. Yonge (1967) stated that *Chama radians* Lamarck may be cemented by either valve, but I was unable to locate any material in the British Museum. Nicol (1952a) reported only one specimen of one thousand *A. arcinella* that appeared to be attached by the right valve.

HINGE DENTITION AND REVERSAL

Munier-Chalmas (1882) and Bernard (1895, 1897) examined the chamid hinge and attempted to homologize it with heterodonts while suggesting a dental formula notation. Dall (1903b) presented an illustration purporting to be a juvenile *C. pellucida* showing radiating cardinals and laterals. Odhner (1919) believed it to be a juvenile *Arcinella;* however I do not consider it to be chamid and have been unable to trace the specimen in the USNM. The first full description of the dentition of juvenile chamids is given by Anthony (1905) and its undoubted heterodont affinity revealed.

Munier-Chalmas (1882) demonstrated that dentition can be ''normal'' or ''inverse'' so that the arrangement of the teeth of the attached valve is similar; whether it be a right or left valve, and the dental elements are mirror images of each other (Yonge 1967). This inversion affects only the shell and hinge morphology; other systems (alimentary, nervous, etc.) are not reversed. Not only are attached bivalves very consistent in the valve by which they attach, but transposition of hinge elements is extremely rare. It has been suggested by various authors that at first adoption cementation may have occurred indifferently by either valve, but would become set later in the history of a species. Termier and Termier (1949) stated that Triassic oysters attached by either valve, but Newell and Boyd (1970) failed to find any well documented cases for Middle and Lower Triassic oyster-like bivalves. Odhner (1919, 1955) thoroughly reviewed the literature and correctly disposed of most reports of hinge reversal. Most inversions involve only part of the hinge structure and are probably teratological. Popenoe and Findlay (1933) could cite no example of complete transposition, though Hanna (1925) mentioned a case of complete inversion in an Eocene *Venericardia* and Eggleton and Davies (1961) noted a small percentage of reversion in some Sphaeriids.

DEVELOPMENT OF ADULT DENTITION

Adult dentition is different from the juvenile heterodont phase. Grant and Gale (1931) state that the hinge teeth ". . . are replaced by rather crude and heavy rugosities. . . ." Added to the impracticability of homologizing adult chamid teeth to the immature condition is the problem of the similarity of dentition of attached or free valves, whether they are right or left. Odhner (1919) accurately stated that current inversion theory "gives no satisfactory explanation of the process by which a right valve may acquire the characteristics of a left one. . . ."

The adult chamid hinge consists of a thick parivincular ligament sunk in a deep pit that may appear as an obtuse escutcheon on the free valve. Three distinct layers are present, consisting of an inner fibrous region covered with a partially calcified lamellar layer and a thin outer periostracal layer. The ligament is attached to substantial nymphs, whose lower margins are much thickened and reflected to envelop part of the ligament. The ligament is invariably more deeply inserted into the attached valve, and the nymphal margins of this valve are more developed than in the free counterpart. The ventral edge of the nymphal margin is crenulated and forms one side of the socket. It has been considered a tooth, and attempts have been made to homologize it with one of the juvenile cardinals. A schematic cross-section of the adult hinge showing the ligament and nymphal ridges is presented in figure 2.

The extensive Allan Hancock Foundation collections from the central eastern Pacific contain over 80 dissoconch and very recently settled chamids of several species. By careful comparison it was possible to assemble probable developmental stages of *Pseudochama* and *Chama*. Camera-lucida drawings are presented in figure 3 of *P. corrugata* Broderip and *Chama* cf. *C. pellucida* (Broderip).

In this material the very early dissoconch stages display two subumbonal cardinals and a smaller posterior lateral in each valve. During development only the lateral maintains its identity, or at least is a direct precursor of the adult structure. The three heterodont teeth remain distinct until cementation and the period of rapid idiomorphic growth. The pit between the cardinals of the free valve deepens and the teeth become buried by a general thickening of the pit edges; the ventral margin receives most deposition and ultimately forms the lateral peg of the free valve. The nymphal thickened margin originates as a group of tubercles that interdigitates with the accretionary mass of the posterior lateral of the free valve.

It is evident that juvenile dentition is identical in arrangement in left and right valve cemented chamids, so that no dental inversion occurs. Probably mechanical constraints, due to the more rapid coiling growth of the attached valve supporting an opercular free valve, lead to the development of a central socket in the attached valve, accommodating a single lateral tooth in its opposite number. This interpretation is essentially a development of Odhner's (1919) suggestion that similarity of arrangement of hinge elements is the result of growth characteristics, but he did

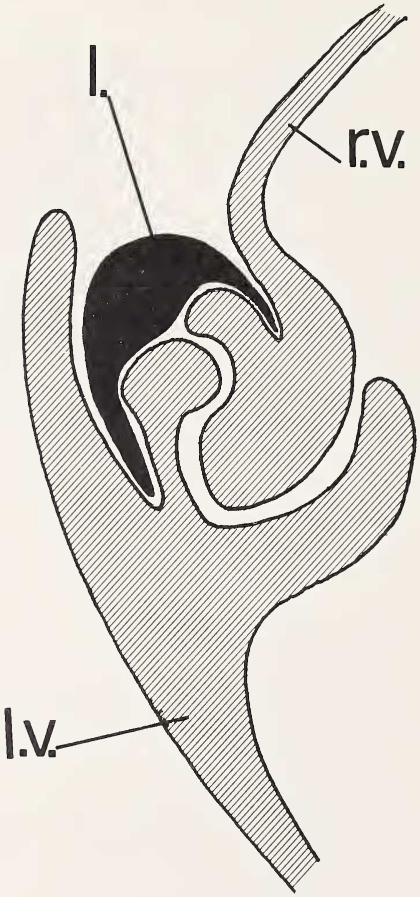

FIGURE 2. Schematic cross section of adult hinge of *Chama*, showing ligamental insertion and nymphal ridges. l. = ligament; l.v. = left valve; r.v. = right valve.

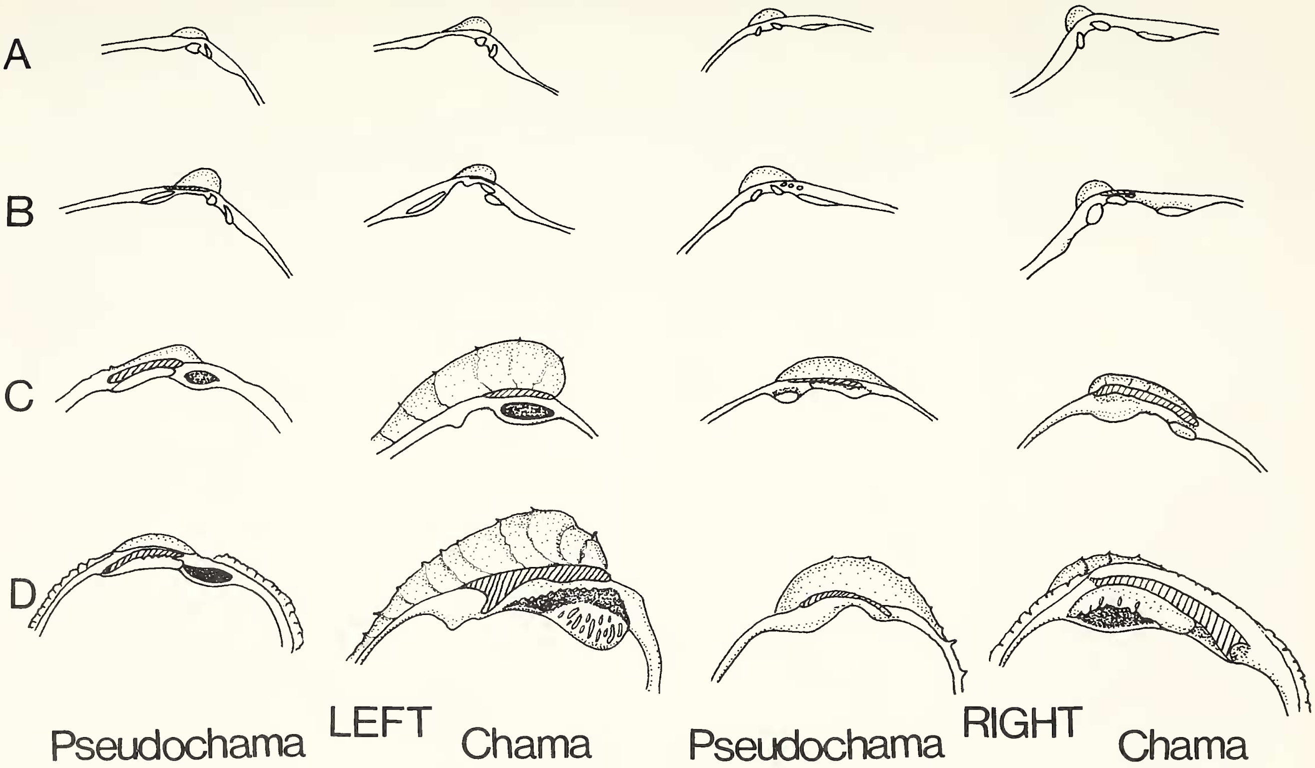

Figure 3. Schematic illustration of postulated hinge development in *Pseudochama* and *Chama*, prepared from camera-lucida drawings.

not recognize the basic identity of the juvenile dentition and proposed a diverse origin for the adult teeth of both groups, which he placed in separate genera.

The concept of separation of adult chamid hinge structures from the juvenile condition is strengthened by the fact that the majority of cemented bivalves are edentulous. Such structures as the sockets of *Spondylus* and the interlocking mechanisms of *Plicatula* and *Dimya* are secondary developments, as well as the loss of classical heterodont dental structures by the adult in *Anodonta* and the Thyasiridae. In these situations the early shell form may provide interesting phylogenetic insights, but the actual systematic placement is based upon adult morphology. Postponed assumption of adult characteristics does not influence generic placement, and it is on this basis that the cemented xenomorphic genus *Hinnites* is separated from *Chlamys,* though the juveniles are indistinguishable.

SHELL GROWTH AND FORM

Bivalve growth being accretionary, the shape of the generating curve is maintained. Shell formation, as Stasek (1963) phrases it, ". . . embodies a functional continuum of past and present." In the majority of bivalves the beaks are the point of origin and geometrical locus from which growth radiates. In chamids, the beaks are the point of origin, but their relative position changes, and finally, the growth origin is transferred to the commissural plane. The continuous secretory mantle border results in the dental elements not remaining marginal, a tendency carried to its extreme in the extinct rudists where the teeth of the free valve are placed subcentrally on the opercular disc.

Chamid growth form includes a pronounced tangential growth component (Yonge 1967). Observation of long developmental series confirms that one-half to three-quarter coiling of the shell occurs rapidly, but this growth pattern continues for a brief time only, and small specimens (3-5 mm) have attained the mature configuration. Subsequent growth is a simple increase in size. Coiling growth also occurs in a number of non-chamid taxa but the shell is usually equivalve, perhaps the earliest example being the Ordovician *Redonia* Rouault, assigned by Chavan (1966) to the carditaceans. The living *Isocardia* is also coiled (Owen 1953), as are some representatives of the Anomalodesmata, notably *Pecchiola,* which was originally considered to be a chamid. However, an elongate spiral design is incompatible with bivalve organization, which requires a large functioning pallial cavity to house the water pumping and food collecting ctenidial apparatus. The majority of bivalves maintain a constant ratio between ctenidial area and body size, however this is not true of spiriform taxa and those with a large subumbonal cavity. Large, old, chamids may nearly halve the proportion of ctenidium to body and there is no doubt this must have profound physiological implications. This problem was not encountered by the rudists, where the large attached valve was filled with porous calcitic deposits, effectively maintaining a proportionately constant shell cavity. Rudists developed further aids to maintaining adequate flow through the pallial cavity, which included perforated upper valves and siphonal notches (Vogel 1960).

SYSTEMATIC POSITION AND RELATIONSHIPS

The many common morphological characters and the ontogeny of the three living chamid genera are suggestive of a single phylogeny. While chamids have long been accepted as a homogenous group, their placement in the Class Bivalvia has been unsure. A marked similarity to the extinct rudists led support for their incorporation within the Hippuritacea (Odhner 1919, Newell 1965, Yonge 1967). Chamids have been thought to have descended from Silurian pachydonts which became cemented to the substrate by one valve in the manner of *Diceras* (Deschaseaux 1952). It is unlikely that the highly evolved porous-shelled Diceratidae could be ancestral to the modern Chamidae.

Rudists are considered to be heterodonts, primarily on dental homology, as no dissoconch stages have been identified from Mesozoic strata. Taylor and Kennedy (1969) and Taylor et al. (1969) confirmed earlier reports that though heterodonts are aragonitic in shell structure, *C. pellucida* Broderip and *P. exogyra* (Conrad) possess a superimposed external calcitic layer, a character shared with rudists. However, this cannot be considered conclusive evidence for affinity (Newell 1965, Yonge 1967). The general similarities to the Hippuritacea are probably the product of convergence as chamids occupied approximately the geographical range of rudists and appropriated the ecological niche vacated by their extinction.

Other authors have traced chamid descent from the Carditacea (Dall 1903b); the Crassatellacea (Böhm 1891); the Lucinacea (Nicol 1952a); and the Veneracea (Fischer 1886). Kennedy et al.(1970), in a wide survey of the shell structure and dental morphology of many fossil and living chamids discussed all these suggestions and demonstrated a most probable relationship to the byssate Carditacea.

Chamids have a comparatively short geological history, the earliest undoubted representatives occur in the Upper Cretaceous of Europe, and bear a strong resemblance to *C. pellucida* Broderip. A period of radiative expansion followed in the Eocene, together with the development of diverse ornamentation. Chamidae are abundant components of the tropical and subtropical shallow water faunules from the Pliocene. The genera *Chama* and *Pseudochama* are widely distributed, but *Arcinella,* which appeared in the Lower Miocene of Florida is endemic to Pacific and Atlantic central America.

EASTERN PACIFIC CHAMIDAE

The roughly north-south axis of the American west coast cutting across temperate and tropical waters yields a rich and diverse chamid faunule. The great majority of species were collected by Hugh Cuming and described by Broderip (1835a) with a few additions by Reeve (1847). Unfortunately the descriptions are overly short and type localities not clear. One problem results from the citation ''Lord Hood's Island,'' which may be either South Pacific or West American. Cuming visited Polynesia in 1827-33 and collected at Lord Hood's Island, now known as South Marutea. The following years Cuming journeyed on the west coast of America collecting at the Pearl Islands, Panama and the Galapagos group, of which the southernmost island was originally Lord Hood's Island, now known as Hood or

Española Island. That Cuming in fact collected here is evidenced by Broderip and Sowerby (1832) in their description of *Stilifer astericola* with a type locality cited as "ad Insulas Galapagos (Lord Hood's Island)." The chamid species with doubtful type localities are *C. pacifica, C. imbricata,* and *C. spinosa.* I had occasion to examine the types and compare them to materials of known distribution and concluded that *C. pacifica* is a well established Indo-Pacific species, the center of distribution being the Solomon archipelago. Broderip states the species is identical to material of Samuel Stutchbury (1797-1859) who collected widely in Australia and Polynesia. A similar situation exists for *C. imbricata;* the type is identical to recently collected Indo-Pacific material and Broderip also mentions Stutchbury materials; however, Broderip also reports a variety of *C. imbricata,* citing the type locality as Insulas Galapagos. This specimen was separated by Reeve (1847) and described under the name *P. janus.* This species is well established in the Galapagos group and bears little resemblance to Broderip's *C. imbricata. C. spinosa* is distinguished by the uniform distribution of sparse spines and scales upon the free valve and resembles nothing in the eastern Pacific province, and is probably Indo-Pacific in origin. The western American chamid fauna appears to be endemic with little relationships to Indo-Pacific representatives, and despite free exchange until the end of the Miocene across the isthmus of Panama no western representatives extend into the Antillean region. The explanation may lie in the almost total extinction in the Pacific of the coral reef biotope.

In this review of eastern Pacific species, literature citations are furnished only to readily available works that are a help to identification. Because of many misidentifications and confusion, particularly in earlier works, published distribution data are to be viewed with reserve; those cited here have been verified with material. The terminology of higher taxa is taken from "Treatise on Invertebrate Paleontology" (R. C. Moore, ed. 1969).

Abbreviations for collections mentioned in the text are identified below:

AHF	Alan Hancock Foundation, University of Southern California
ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
LACM	Natural History Museum of Los Angeles County
MNHN	Museum National D'Histoire Naturelle de Paris
MCZ	Museum of Comparative Zoology, Harvard
SDSNH	San Diego Society of Natural History
USNM	National Museum of Natural History, Washington, D.C.

SYSTEMATIC REVIEW

SUPERFAMILY CHAMACEA LAMARCK 1809

Shell cemented, at least temporarily, to substrate. Umbones prosogyrate, ligament parivincular, adult dentition consisting of a large lateral process in the upper valve inserted in a deep pit on opposite valve. Sculpture generally well developed, consisting of spines sometimes conjoined into concentric frills. Pallial line entire, adductor muscle scars subequal. Upper Cretaceous to Recent.

FAMILY CHAMIDAE LAMARCK 1809

Shell characters as in Superfamily. Variable and xenomorphic. Predominantly among shallow warm water epifauna. The shell may be ponderously thickened in old specimens and external characters frequently obliterated by abrasion and the activity of shell borers. Anatomically this family is conservative. Mantle extensively fused except for a small pedal gape and two small delicate siphons formed solely from the inner mantle fold. Adductor muscles elongate, nearly subequal. Foot reduced, laterally compressed. Ctenidium comprising a large inner demibranch with a much smaller outer demibranch. Lamellae plicate, synaptorhabdic, filaments connected by substantial interfilamental junction. Interlamellar junctions short and numerous. Labial palp small, generally asymmetrical, with 12-20 palpar ridges. Mouth small, leading to short, longitudinally plicated oesophagus. Stomach large, divided by prominent ventral ridge. Style pouch and midgut conjointed. Intestine short, piercing heart ventricle.

The anatomical characteristic of the Chamidae suggests that they are adapted to waters with little suspended materials. The alimentary system is modified for the acception of fine particulate materials. Representatives of the family occur on hard substrates removed from zones of sedimentation. Geologically this group is probably indicative of warm water as those few representatives extending to cooler waters are all small and lack pronounced sculptural processes.

There are three West American genera.

GENERIC KEY TO THE WEST AMERICAN CHAMIDAE

1. Shell nearly equivalve, lunule pronounced; not attached	*Arcinella*
Shell inequivalve, no lunule; cemented	2
2. Shell attached by left valve, nepionic shell small	*Chama*
Shell attached by right valve, nepionic shell large	*Pseudochama*

GENUS *CHAMA* LINNÉ 1758

Type (subsequent designation: Schmidt 1818) *Chama lazarus* Linné 1758

Shell thick, porcellaneous, sometimes with waxy translucent outer layer. Shell cemented by left valve. External surface smooth or ornamented with irregularly placed concentric and radial processes. Attached valve with hyote-type spines. Commissural margin sometimes produced. Dentition consisting of a single broad tooth-like process in the right valve, fitting into socket in left valve. Nepionic shell small, with typical heterodont dentition, externally ornamented with concentric and radial sculpture. No abrupt transition of growth pattern at the post-neanic stage. Anatomy as for Superfamily.

Subgenera proposed in *Chama,* such as *Cipliacella* Vincent, 1928 (Type *C. pulchra* Ravn 1902) or *Psilopus* Poli 1795 (Type *C. gryphoides* Linné 1758) are based upon minor variations not significant above the species level.

Twelve species occur in the eastern Pacific, the majority in the Panamic province.

Artificial Key to West American *Chama*

1.	Interior shell not colored	2
	Interior of shell colored	8
2.	Both valves strongly arched, attachment area small	3
	Upper valve flat, attachment area large	4
3.	Exterior ornamented with many short narrow spines	*C. corallina*
	Exterior ornamented with few long broad arched spines	*C. sordida*
4.	Exterior ornamented, no distinct color pattern	5
	Exterior smooth, with uniform brown lines	*C. venosa*
5.	Shell waxy, with wide, minutely crenulated commissural shelf	6
	Shell porcellaneous with narrow, coarsely crenulated commissural shelf	7
6.	Shell laterally elongated, exterior with short uniform frills, fused into concentric wrinkles	*C. pellucida*
	Shell vertically elongated or round, exterior with irregular thin frills, not fused into concentric wrinkles	*C. arcana*
7.	Exterior white spines uniform, fusing into concentric frills	*C. squamuligera*
	Exterior colored, spines irregular, separate	*C. garthi*
8.	Internal color limited to narrow marginal band	9
	Internal color diffused	10
9.	External sculpture lacking or of narrow spines	*C. buddiana*
	External sculpture of broad, striated foliations	*C. frondosa*
10.	Internal color a diffuse marginal flush, or on anterior adductor muscle scar	*C. mexicana*
	Internal color extensive	11
11.	Interior purple, hinge teeth bright coral red	*C. echinata*
	Interior yellowish red, hinge teeth white	*C. tinctoria*

Chama arcana new species

Figures 4 a, b

Chama pellucida auctt., not Broderip 1835a:149; Keep 1888:182, fig. 155 (as of Sowerby); Arnold 1903:130 (Pliocene, Pleistocene of California); Arnold 1910:38 (Upper Miocene of California); Grant and Gale 1931:279; Soot-Ryen 1931:314 (Galapagos Islands); Smith and Gordon 1948:173.

Diagnosis: The new species can only be confused with *C. pellucida* Broderip, but the commissural shelf is wider and the latter lacks the streaks of bright color often present on the upper valve. The sculpture of *C. arcana* is irregular, thin, and periodically drawn out into longitudinally striated lamellae, which are not present in *C. pellucida,* where the sculpture is more uniform and subdued. The shell of *C. pellucida* is proportionately thicker and tends to be anteroposteriorly elongated, while in *C. arcana* it is subcircular or dorsoventrally elongated. A distinct, but small, pallial sinus is present just below the adductor muscle in *C. pellucida,* which is absent in the new species.

Description: Shell interior porcellaneous, white, exterior waxy translucent. Outline variable, depending upon habitat, either round or dorsoventrally elongated. Cemented to substrate by wide area of left valve. Exterior sculpture often abraded and encrusted, color white, sometimes with streaks of pink or red particularly on posterior of right valve. Sculpture of either valve consisting of close-set foliations irregularly joined into thin translucent concentric lamellae, with several radial rows of larger prolongations. Ligament deeply sunk and placed on a substantial nymph. Dental processes not highly developed, nymphal ridge of left valve with a strongly developed longitudinal groove. Shell margins minutely denticulated. Commissural shelf broad, lacking inner layer, sometimes iridescent. Adductor muscle scars large. Pallial lines shallow, entire.

Holotype measurement: Length 55, height 64, width 39 mm.

Type locality: Newport Bay, California (33°37′N, 117°55′W). Intertidal —Collected March 1965 by J. McLean.

Holotype deposition: LACM 1723.

Geographic range: Yaquina Point, Oregon (44°N) to San Juanico Bay, west coast of Baja California (26°N).

Bathymetric range: In Oregon and California this species occurs from the low intertidal level down to 50 meters. In its southern range it is always subtidal, down to 80 meters.

Habitat: Clear water, often in nooks and crannies in exposed zones. Attached to a solid substrate, rocks, pilings, breakwaters, subtidally often attached to gravel.

Etymology: The specific name is derived from the Latin adjective *arcanus* (secret), referring to the long hidden distinctness of this species from *C. pellucida.*

Discussion: This species is common in the California Province, first appearing in the Upper Miocene (Arnold 1910) and more frequently in the Pliocene and Pleistocene (Arnold 1903). It occurs higher in the intertidal zone than other chamids and is frequently found on pilings and other man-made objects. It has the most northern range of the genus, and, in common with some other cool water bivalves, extends down the coast of Baja California. Dall (1921) included the Galapagos Islands; this is probably not correct as USNM does not contain specimens from Galapagos. Soot-Ryen (1931) also recorded this species from the Galapagos group. *C. arcana* is entirely absent from the tropical Panamic province and its congener *C. pellucida* Broderip appears in similarly cool southern waters. These two species are closely related, but consistent differences in sculpture and shell shape separate them as discussed above.

Of the West American chamas, *C. arcana* and *C. pellucida* occupy the coolest waters. Lowenstam (1954) first noted the presence of an outer calcitic layer in *C. pellucida* and later suggested (Lowenstam 1963) that the aragonitic outer layer of warm water chamids is transformed to prismatic calcitic structure in a cool water environment. Taylor and Kennedy (1969) confirmed the calcitic external layer, but showed it to be an extra layer superimposed upon the normal aragonite shell of the Superfamily. This fact, coupled by their belief that *C. pellucida* is distributed transequatorially led Taylor and Kennedy to reject Lowenstam's hypothesis. In an appendix Taylor and Kennedy (1969) noted a calcitic layer in *Pseudochama exogyra* and suggested that this species is conspecific to *C. pellucida.* I cannot agree with these authors that the occurrence of a calcitic outer layer in these three species is sufficient grounds for combining them into a single taxon. It is well established that warm water bivalves tend to display a higher proportion of aragonite than cold water representatives, and Lowenstam's suggestion should be reconsidered, not on an individual ecomorphic basis but in a phylogenetic sense.

Chama buddiana C. B. Adams 1852

Figures 5 d, e

Chama buddiana C. B. Adams 1852:253 (Type locality: Panama Bay, 7°N. Syntypes MCZ); Turner 1956:36, pl. 20, figs. 7, 8 (designation of lectotype MCZ 190150); Olsson 1961:224, pl. 34, figs. 2-2c; Emerson and Hertlein 1964:348 (Pleistocene of Mexico); Keen 1971:147, fig. 346.

External surfaces pink to deep red, ornamented with irregular radial rows of small triangular white spines. Interior white with pinkish red marginal band. Shell margin finely crenate.

Discussion: The exterior coloration, the contrasting small triangular white spines interspersed with a few large ones in irregular rows, together with the marginal band of color distinguish this species.

This is the largest and most abundant chamid occurring off Panama but it is uncommon elsewhere. The Port Parker location, from the Allan Hancock Stations is a northward extension of the confirmed range. Dall's (1921) record of this species from California is certainly in error, probably stemming from the fact that Adams also cited material collected by Lt. Green at Guaymas. It is clear that Adams intended to describe those specimens personally collected at Panama but mentions material he considered identical.

Carpenter (1864) placed his *C. frondosa fornicata* in the synonymy of this species. After examining the types I consider that these species are in fact not synonymous, and that Carpenter's material is referable to *C. mexicana* Carpenter, 1857. *Chama rubropicta* Bartsch and Rehder, 1939 is an immature *C. buddiana* Adams, 1852.

C. buddiana is found in the low intertidal zone to 2 meters, generally attached to rock on large boulders. It ranges from Port Parker, Costa Rica (11°N) to Cape San Francisco, Ecuador (0°39′N). Also reported from Clipperton Island and the Galapagos Group (Albermarle, Narborough, and Indefatigable Islands). Emerson and Hertlein (1964) recorded this species from the Mexican Pleistocene.

Chamma corallina Olsson 1971

Figures 6 c-f

Chama corallina Olsson, 1971:39, figs. 7-10. (Type locality: Off Punta Escondido, Gulf of Panama, 7°59′N, 78°30′W, in 55 meters. Holotype USNM 701157); Keen 1971:197, fig. 346a.

Shell with both valves inflated, attachment area small. Exterior pinkish brown to red. Interior white. Surface sculpture of fine radial riblets with irregular sharp spines. Shell margin crenulated.

Discussion: The small size, rotundity of outline and concentric wrinkles with small sharp spines readily distinguish this rare species. Mr. and Mrs. E. E. Wahrenbrock collected several specimens from trash fish dumps in Mazatlan that had been trawled off the Sonora coast of Mexico.

This species is most frequently attached to small pebbles or calcareous polychaete tubes in 18 to 95 meters. It ranges from the Sonoran coast of Mexico (23°N) to Punta Escondido, Gulf of Panama (7°59′).

Chama echinata Broderip 1835

Figures 7 a-f

Chama echinata Broderip 1835a: 150 (Type locality: Puerto Portrero, Bay of Guayaquil, Ecuador, 2°11′S. Syntypes BM(NH) 1950. 11.1.20-22); Broderip 1835b:305, pl. 39, fig. 5; Reeve 1847: pl. 7, fig. 35; Stearns 1893:375; Clessin 1889:14, pl. 6, fig. 2; Keen 1971:147, fig. 347.

Chama coralloides Reeve 1847: pl. 4, sp. 18 (Type locality: Puerto Portrero, Ecuador, 2°11′S. Holotype BM(NH) no. number).

Chama delesserti Chenu 1846: pl. 6, fig. 4 (Type locality: Puerto Portrero, Bay of Guayaquil, Ecuador, 2°11′S. Holotype BM(NH) 1950.11.1.20).

Exterior yellowish white, sculpture of many short irregular spines, often totally abraded in mature specimens. Interior deep purple, hinge teeth bright coral red. Juvenile specimens display only the purple interior, the red hinge appearing later.

Discussion: Reeve (1847) illustrated *C. echinata* but separated two worn specimens of Broderip's type series to erect *C. coralloides*. Chenu (1846) reproduced Broderip's (1835b) figure of *C. echinata* under the new name *C. delesserti*. Carpenter (1857a) pointed out this confusion and correctly surmised that Chenu's species should also be placed in synonymy.

The deep purple of the interior, contrasting with the bright coral hue of the hinge teeth distinguishes this species from all other American chamids. The outside of the shell is frequently abraded and overgrown, attached to large rocks from the low intertidal zone to 25 meters. The geographical range is from Angel de la Guarda Island, Gulf of California (29°N) to Huanape Island, Northern Peru (8°34′S).

Chama frondosa Broderip 1835

Figures 8 a-c

Chama frondosa Broderip 1835a: 148 (Type locality: Isla La Plata, Ecuador, 1°18′S, BM(NH) 1950.11.1.55); Broderip 1835b:302, pl. 38, fig. 1; Reeve 1847: pl. 1, fig. 1a; Stearns 1893:375; Lamy 1927:314; Durham 1950:73, pl. 17, figs. 5, 6 (Pliocene to Recent of Mexico); Emerson 1960:6 (Shell middens of Mexico); Olsson 1961:225, pl. 34, figs. 1a, b, pl. 86, fig. 2; Keen, 1971:147, fig. 348.

Chama pacifica Carpenter (Gould MS) 1847, not Broderip 1834 (*fide* Carpenter 1857b).

Chama parasitica Rocheburne 1895:243 (Type locality: San Jose Island, Gulf of California, Mexico, 25°N. Holotype MNHN).

Shell heavy, pinkish white, external sculpture of wide radially striated foliations. Interior white, with narrow pink or purple marginal band.

Discussion: This infrequently encountered chamid is the only West American species with foliated spines. It occurs cemented to rocks and large boulders, extending from the subtidal zone to 25 meters. The geographic range is from southern part of the Gulf of California at La Paz (24°30′N) to Salango Bay, Ecuador (1°35′N). I have not seen genuine material from the Galapagos Islands and records from the outer coast of Baja California and California are certainly misidentifications. This is a warm water species and there is some doubt as to its northern extent, as the La Paz record is based upon a single specimen.

Chama garthi new species

Figures 9 a, b

Chama spinosa auctt., not Broderip 1835; Carpenter 1857a:90; Strong and Hanna 1930:15.

Diagnosis: The species may be confused with *C. squamuligera* Pilsbry and Lowe, but is easily distinguished by the bright external coloration and by the spines, which never fuse into crenulated frills.

Description: Shell small, rounded, exterior irregularly mottled with purplish red. Attachment area small. Left valve deeply cupped, right valve nearly flat. Right valve covered with dense radial rows of short imbricated free spines; left valve with fewer wider spines. Interior white or stained light brown; margins delicately crenulated.

Holotype measurement: Length 19.5, height 23.7, width 15 mm.

Type locality: Octavia Bay, Colombia (6°50′N, 77°41′10″W). Shallow water. Allan Hancock Station 435-35, January 28, 1935.

Type deposition: AHF 167 (Holotype). AHF 168 (Paratype).

Geographic range: Type locality and Salango Island, Ecuador (1°35′S).

Bathymetric range: Intertidal level to 22 meters.

Habitat: Rock and coral.

Etymology: The species is named for John S. Garth of the Allan Hancock Foundation in small recognition for his inestimable services to Central American malacology while accompanying all the Hancock Pacific Expeditions Velero III cruises (1931-1941).

Discussion: The external coloration and delicate imbricated spines make *C. garthi* the most elegant of West American chamids. There is a superficial similarity to juvenile *C. echinata* Broderip, but the new species displays a wide commissural shelf, entirely lacking in young *C. echinata* and the attached valve of *C. garthi* carries a few wide spines, rather than the many small spines of *C. echinata*.

Chama maculata Clessin 1889

Chama maculata Clessin 1889:43, pl. 4, figs. 4, 6.

The brief description and indistinguishable illustration relegate this species to a *nomen dubium* status. The type locality is the Strait of Magellan. It is highly improbable that these cold waters support any representative of the Chamidae. The literature yields no other mention of a chamid occurring south of approximately 33°S. Unfortunately the Clessin collection, housed in the Stuttgart Museum, was totally destroyed during the Second World War.

Chama mexicana Carpenter 1857

Figures 10 a-c

Chama frondosa mexicana Carpenter 1857a:87 (Type locality: Mazatlan, Mexico, 23°N. Syntypes BM(NH) Carpenter Collection Tablets 425-438); Hertlein and Strong 1955:114 (Galapagos Islands); Hertlein and Emerson 1956:165 (Pleistocene of Mexico); Keen 1971:147, fig. 349 (as *C. mexicana*).

Chama frondosa fornicata Carpenter 1857a:89 (Type locality: Mazatlan, Mexico, 23°N, Syntypes BM(NH) Carpenter Collection Tablets 439-443); Keen 1968:397, pl. 56, figs. 31 a, b, figs. 35 a, b.

Chama frondosa (*var β*) Broderip 1835a:149 (Type locality: Mazatlan, Mexico, 23°N. Type not located in BM(NH); Broderip 1835b:302, pl. 38, fig. 2.

Chama producta Broderip 1835a:150 (Type locality: Gulf of Tehuantepec, Mexico, 16°N. Holotype BM(NH) 1950.1.1.60); Broderip 1835b:305, pl. 39, fig. 4: Reeve 1847, pl. 3, fig. 13; Clessin 1889:20, pl. 10, fig. 1: Lamy 1927:314; Keen 1971:899 (Nomen oblitum).

Chama purpurascens Tryon (Conrad MS) 1872:117 (as synonym of *C. frondosa* Broderip 1835); Pilsbry and Vanatta 1902:551 (Galapagos Islands, as *Chama frondosa purpurascens* Conrad).

Chama compacta Clessin 1889:25, pl. 10, fig. 4 (Type locality: unknown. Type destroyed in WW. II).

Shell exterior pink to deep red, with many small, and two radial rows of larger spines. Interior white to yellowish. There is an indistinct flush of pinkish purple around the anterior adductor muscle scar and part of the shell margins. Gerontic specimens generally riddled by borers and with spines abraded.

Discussion: This species is readily separable from other West American chamids by the irregular internal purple red flush, which generally spreads to include the anterior adductor muscle scar.

There is some confusion in the literature concerning the type locality of *C. mexicana*. Carpenter (1857a) recognized that his specimens were identical to Broderip's *C. frondosa var β*, and intended merely to apply an acceptable name to it. In such a situation, Broderip's specimen must remain the type, unless a case can be made to suppress it entirely. Such a case can be made on the basis that symbols have no nomenclatural status or that Broderip's taxon may be considered a *species inquirenda*. The extreme brevity of Broderip's description would also favor considering it a *nomen dubium*. I was unable to locate *C. frondosa var β* in the Cuming Collection, and incline to accept Carpenter's material as syntypic, or at least plesiotypic.

Comparison of the paratype of *C. producta* Broderip (Fig. 10a) to the types of *C. frondosa mexicana* and *C. frondosa fornicata* convinced me they are synonymous and well removed from *C. frondosa* Broderip. However, Reeve (1847) thought *C. producta* to be identical to *C. iostoma* Conrad 1837, a species indigenous to Hawaii (Dall et al. 1938). Keen (1971) did not accept this view, and rejected *C. producta* on the basis of discrepancies in the description. Under guidelines adopted by the 1972 ICZN Commission meeting in Monaco the name is not available for nomenclatural purposes. In the unlikely event that it is proven desirable to reinstate *C. producta* Broderip, formal petition will have to be made to ICZN.

The species occurs on small cobbles and boulders, nearly always on a sandy substrate, from the middle intertidal zone to 80 meters. The geographical range is the head of the Gulf of California, Mexico (31°N) to San Jose point, Guatemala (13°46′N).

Chama pellucida Broderip 1835

Figure 4 c, d

Chama pellucida Broderip 1835a:149 (Type locality: Iquique, Chile, 20°13′S, in 17-20 meters. Syntypes BM(NH) 1950.11.1.63-65); Broderip 1835b:302, pl. 38, fig. 3; Reeve 1847: pl. 6, fig. 32: Clessin 1889:18, pl. 8, figs. 3-4; Lamy 1927:345; Olsson 1961:225, pl. 33, figs. 2, 2a, pl. 34, fig. 5; Marincovich 1973:11, fig. 10; *not* Smith and Gordon 1948:173; *part* Osorio and Bahamonde 1970:198 (Juan Fernandez Islands); *not* Hertlein and Grant 1972:227, pl. 43, figs. 12, 15.

Chama chilensis Philippi 1887:173, pl. 37, fig. 9 (Type locality: Pliocene of Laguna de Cahuil, Chile, 34°30′S, 72°01′W. Holotype MNHN no number).

Shell rounded, generally longitudinally elongated. Sculpture of short, translucent fluted spines, fused into concentric ridges. Exterior white or pink, sometimes dashed with red. Interior white, margins sharply crenulated. Commissural shelf wide. Small pallial sinus present.

Discussion: This species is close to the northern *C. arcana* new species, and possibly bears the same relationship to it as do Caribbean congeners of central eastern Pacific species. Both *C. arcana* and this species are inhabitants of cool waters, effectively separated by the warm equatorial zone since Miocene times. The more elongate form, proportionately thicker shell, and short concentric spines fused into ridges differentiate this species from its northern relative.

It appears that Keep (1888) first confused northern representatives with *C. pellucida* which is restricted to the Peruvian province and does not occur north of Paita. *Chama chilensis* Philippi from the Pliocene of Chile is certainly this species. Californian fossil materials, some as early as Late Miocene are all referable to *C. arcana* new species. Odhner's (1922) reference to *C. imbricata* Broderip, from the Juan Fernandez Islands, is actually to *C. pellucida.*

This species occurs high in the intertidal zone to 30 meters, most frequently nestling in fissures of rocks, or on pilings. The range is from Paita, Peru (5°15′S), to Tocopilla, Chile (22°S). It is also abundant in the low intertidal zone of the Juan Fernandez Islands (33°S).

Chama sordida Broderip 1835

Figures 6 a, b

Chama sordida Broderip 1835a:151 (Type locality: Isle of Cuna, Central America. Syntypes BM(NH) 1950.11.1.52-53); Broderip 1835b:306, pl. 39, figs. 8, 9; Keen 1971:149, fig. 35 (Right figure only).

Exterior reddish brown, the overall pattern of small radial riblets sparsely interspersed with large imbricated spines. The interior white, with the exterior color showing through. The margin is finely crenulated.

Discussion: The radial ribs and few large spines make it unlikely to confuse the identity of this elegant species. This is not *C. digueti* Rochebrune as suggested by a number of workers, which has an entirely different sculpture and should be assigned to *C. venosa* Reeve.

This species is generally attached to calcareous organisms and occurs from the subtidal zone to 45 meters. The geographic range is from Angel de Ia Guarda Island, Gulf of California, Mexico (29°39′N), to Gorgona Island, Colombia (3°01′N).

I have been unable to trace the original type location, given as Isla Cuna, America Centrali. The latter was in contemporaneous use for the region north of Panama Bay, approximately 9°N to 15°N. Isla Punta Icaco, Nicaragua (12°33′N, 87°16′W) is here designated the type locality.

Chama squamuligera Pilsbry and Lowe 1932

Figures 9 c, d

Chama spinosa auctt., not Broderip 1835a (in part).

Chama squamuligera Pilsbry and Lowe 1932:103, pl. 14, fig. 10 (Type locality; San Juan del Sur, Nicaragua, 11°15′N, 85°53′W. Holotype ANSP 155623, Paratypes SDSNH 475a,b); Durham 1950:73, pl. 17, fig. 3, 6 (Pliocene to Recent of Mexico); Hertlein and Allison 1966:139 (Clipperton Island 10°17′N, 109°13′W); Keen 1971:149, fig. 351.

Chama rubropicta Bartsch and Rehder 1939:13, pl. 3, figs. 6-10 (Type locality: Clipperton Island, 10°17′N, 109°13′W. Holotype USNM 472553)

Chama squamuligera rubropicta Bartsch and Rehder. Hertlein and Emerson 1953:350 (Clipperton Island); Salvat and Ehrhardt 1970:227 (Clipperton Island).

Shell small, pure white to yellowish. Exterior sculpture of thin broadly imbricated spines conjoined into concentric frills. In worn specimens the frills are reduced to concentric wrinkles. Interior white, margin finely crenulated. Commissural shelf wide, often granulose.

Discussion: This small nearly colorless species is characterized by the many spines, tending to fuse into irregular concentric lamellae.

When proposing this species Pilsbry and Lowe considered it very similar to *C. spinosa* Broderip (Fig. 9e), separating it on a purely geographical basis. *C. spinosa* has been listed in the West America fauna (Strong and Hanna 1930) —another legacy from the Cuming location "Lord Hood's Island," in fact South Marutea, as Broderip's species is clearly identifiable with South Pacific material and probably synonymous to *C. asperella* Lamarck 1835, which has a few months' priority. It is probable that *C. flavida* Clessin 1889 described from Panama with no suggestion whether Pacific or Caribbean will prove to be this species. Clessin's description and illustration do not match Caribbean materials I have examined; they do, however, conform to the yellowish phase of *C. squamuligera.* Should they prove synonymous Clessin's name will have priority, unless a case for treating it is as a *nomen oblitum* can be made.

This species is frequently found nestling in dead bivalve shells, or on small pebbles from the subtidal zone to 20 meters. It ranges from Gonzaga Bay, Gulf of California, Mexico (29°47′N), to Bahia Honda, Panama (7°43′N), also in the Galapagos Group (Indefatigable and Barrington Islands) and Clipperton Island.

Chama tinctoria new species

Figures 5 a-c

Chama pacifica auctt., not Broderip 1835 (Holotype BM(NH) 1950. 11.1.54, Indo-Pacific); Tryon 1872:119; Clessin 1889:15, pl. 7, fig. 2. Not *chama pacifica* Carpenter (Gould MS) 1857b (synonym of *Chama frondosa* Broderip 1835).

Chama broderipi auctt., not Reeve 1847 (Holotype BM(NH) 1952.4.9.1, Indo-Pacific); Tryon 1872:119; Lamy 1927:319 (as *Chama pacifica broderipi* Reeve 1847).

Diagnosis: This variable species can only be confused with *C. buddiana* Adams, but is more brightly colored and bears more spines on the upper valve, while the lower valve displays uniform radial costae never found on *C. buddiana*. Inside, the new species is more highly colored, and, though *C. buddiana* may be lightly maculated with pink or lilac, it never displays the bright rose brown. *C. tinctoria* has no colored marginal band.

Description: Shell very inequilateral, exterior of right valve brightly colored, with purple radial lines on anterior region, posterior white, central portions pink. Left valve exterior uniform brownish red. Sculpture of right valve consisting of short imbricated scales, white at the base and yellowish red at the tips. Left valve covered with shallow uniform radial costae, with sparse imbricated scales. Interior of right valve white, with a purple to brown patch. Interior of left valve white, flushed light brown to rose red with a darker border. Margin uniformly crenulated.

Holotype measurement: Length 32.5, height 37, width 29 mm.

Type locality: Bahia Honda, Panama, 7°43′16″N, 81°32′55″W, Allan Hancock Foundation "Velero" Station 249-34, in 28-37 meters.

Type deposition: AHF 169 (Holotype). AHF 170 (Paratype).

Etymology: Named from the Latin adjective *tinctorius*—of dyeing, to draw attention to the remarkable exterior and interior color combination.

Geographic range: Gulf of California (?). Tres Marias Islands, Mexico (21°26′N), to Bahia Honda, Panama (7°43′N).

Bathymetric range: 15 to 92 meters.

Habitat: Rocks and bivalve shells.

Discussion: Carpenter (1857b) cited "*C. pacifica* Gould" off the west coast of America and synonymized it with his *C. frondosa mexicana*. I have been unable to trace the specimen or any reference in Gould's publication to *C. pacifica* and consider it an MS name; however, it is possibly a *lapsus* for *C. pacifica* Broderip, which has appeared with its synonymous *C. broderipi* Reeve in eastern Pacific literature. Diguet in 1894 collected from the Gulf of California a large chamid he identified with *C. broderipi* Reeve, 1847. Lamy (1927) reviewing the collections in the Paris Museum cited Diguet's material as *C. pacifica broderipi* Reeve and accepted a pan-Pacific distribution. On examination of this specimen I concluded it is a distinct species with only superficial resemblance to Indo-Pacific representatives, and identical to two lots in the Allan Hancock Foundation collected off Mexico and the Gulf of Panama. As Diguet's material lacks a specific type locality and despite its large size, appears immature, I designate the Allan Hancock Foundation Panamic specimen as the type.

Chama venosa Reeve 1847

Figures 11 c-e

Chama venosa Reeve 1847: pl. 7, sp. 34 (Type locality: not stated. Syntypes BM(NH) 1950.11.1.4-6); Clessin 1889:36, pl. 16, fig. 6; Lamy 1927:341; Keen 1971:149, fig. 352.

Chama diqueti Rochebrune 1895:243 (Type locality: San Jose Island, Gulf of California, Mexico, 25°N. Syntypes MNHN); Keen 1971:149, fig. 350 (as *Chama sordida* Broderip 1835, left and center figures only).

Shell exterior smooth, with a few short scattered spines, white with an elegant pattern of fine reddish brown lines. Margins slightly and irregularly crenulated.

Discussion: This small species with parallel fine lines on the smooth shell cannot be mistaken. Superficially it is close to *P. janus* Reeve, but in this species the elegant fine lines are replaced by brown staining of the depths of radial striae and the upper valve demonstrates two distinct sculpture patterns. Keen (1971) illustrated the holotype of *C. digueti,* synonymizing it with *C. sordida* Broderip. Her illustration is one of three single specimens in the Paris Museum considered by Rochebrune when proposing his new species, but the description is based upon a syntypic cluster of 4 specimens. Lamy (1927) states this group to be the type lot and I believe Rochebrune drew attention to mutual fusion at the start of his description ''Testa aggregata . . .'' as the cemented nature of chamids was well established by then. I follow Lamy (1927) in considering *C. digueti* to be a junior synonym of *C. venosa* as it bears the flattened upper shell valve and reddish brown lines of the latter species and entirely lacks the bi-convex shape and long imbricated spines of *C. sordida.* A fine specimen in the d'Orbigny collection from Paita, Peru (BM(NH) 1954. 12.4.820) is undoubtedly this species.

This species has been collected on wharf pilings and dead shell from the subtidal zone to 4 meters. Distribution is centered in the Gulf of California, Mexico from 28°N and south possibly to Paita, Peru (5°S). Guaymas, Sonora, Mexico (29°52′N, 111°06′W), is here designated the type locality.

GENUS *ARCINELLA* SCHUMACHER 1817
(= *ECHINOCHAMA* FISHER 1887)

Type (monotype) *A. spinosa* Schumacher 1817 = *A. arcinella* Linné 1767.

Shell nearly equivalve, briefly cemented by right valve during early growth. Sculpture of radial rows of long, partially recurved spines, interspaces pitted, resulting in a reticulated appearance. Beaks prominent, prosogyrate. Lunule deeply impressed. Ligament short, deeply buried. Hinge elements as in *Chama* but more delicate. Nepionic shell distinctly demarcated, sculptured with concentric ridges.

Arcinella was first proposed by Oken (1815) for a carditid genus and is a senior homonym of *Arcinella* Schumacher 1817. In 1956 (Opinion 417) the ICZN rejected Oken as non-binomial, so *Arcinella* Oken no longer preoccupied Schumacher's genus. However, *Echinochama* Fischer 1887 is a synonym of *Arcinella* Schumacher; both cited *Chama arcinella* Linné 1767 as the type of the genus. Keen

(1962) summarized the situation, and pointed out that a rejected senior homonym has no status unless subsequently validated. On the basis of strict priority she proposed the use of *Arcinella* Schumacher. Nicol (1965) felt there may be some objection to adopting *Arcinella* and it could be considered a *nomen oblitum*. As no application has been made to the ICZN to retain *Echinochama* Fisher, and *Arcinella* Schumacher has appeared several times in the literature since Keen's 1962 article, it may be considered established in the taxonomy.

The gross external anatomy of *Arcinella* has already been discussed and appears very close to *Pseudochama,* except the foot is longer and the pedal aperture rather more ventral. The nepionic shell is similar to *Pseudochama* as is the abrupt post-neanic change in shell sculpture.

The taxon is confined to central America, appearing in the Early Miocene of Florida (Nicol 1952a). Speciation and distribution has occurred in the Caribbean, but the group is poorly developed on the Pacific side.

One eastern Pacific species:

Arcinella californica (Dall 1903)

Figure 6 g

Echinochama californica Dall 1903a:950, pl. 62, fig. 5 (figure only); Dall 1903b:1404, 1406. (Type locality: Cedros Island, Baja California, Mexico, 28°N, in 24 meters. Holotype USNM 96452); Keen, 1971:149, sp. 353 (as *Arcinella californica*).

Echinochama arcinella californica (Dall), Nicol 1952a:806, pl. 119, fig. 8; Olsson 1961:227, pl. 34, fig. 3.

Shell equivalve, whitish yellow, anterior portion produced into a lobe, lunule deep. Sculpture of symmetrical radial rows of long, sometimes recurved spines. Interior white, border finely crenulated.

Discussion: This rare species is closely related to the Caribbean *A. arcinella* (Linné 1767) but may be distinguished by the more produced anterior lobe, longer spines and more distinct surface pattern. Nicol (1952a) considered western representatives as only a subspecies of the Caribbean form and proposed a new subspecies *A.a. olssoni* for Pliocene or Pleistocene Pacific Panama material displaying particularly large flat spines.

The type locality of *A. californica* cited by Dall is Cerros (now Cedros) Island, situated on the outer coast of Baja California. Though Pilsbry and Lowe (1934) refer to single specimens dredged off Mexico at Manzanillo (19°N) and Acapulco (17°N) and the S. S. Berry collection contains several specimens from Angel de la Guarda Island, Gulf of California (29°N), the main distribution appears to be south of the Gulf of Tehuantepec (15°N). This species is represented in the Allan Hancock Foundation holdings by several small valves from Port Utria, Colombia (5°N). The geographic range is from Cedros Island, Mexico (28°N) to Port Utria, Columbia (5°58′N). Juveniles are generally attached to calcareous organic structures, particularly gastropod shells. The adults lie free on the substrate in 25 to 77 meters.

GENUS *PSEUDOCHAMA* ODHNER 1917

Type *Chama cristella* Lamarck 1819 (subsequent designation: J. Gardner 1926, see Nicol (1952b)).

Shell attached by right valve. Nepionic shell large, subquadrate. Other characters as of the family. Oligocene to Recent.

Seven eastern Pacific species:

ARTIFICIAL KEY TO WEST AMERICAN *PSEUDOCHAMA*

1.	Shell interior white, sometimes with brown patch	3
	Shell interior extensively streaked or uniformly colored	2
2.	Color streak rose or red	*P. clarionensis*
	Shell with extensive purple stain	*P. corrugata*
3.	Upper valve sculpture medially bisected	*P. janus*
	Upper valve sculpture not bisected	4
4.	Shell inner margins smooth or finely crenated	5
	Shell inner margins uniformly coarsely ridged	*P. saavedrai*
5.	Shell lacking obvious periostracum	6
	Shell with thin brownish periostracum	*P. dalli*
6.	Sculpture of numerous concentric lamellae and spines	*P. exogyra*
	Sculpture of irregular fluted broad spines	*P. panamensis*

Pseudochama clarionensis Willett 1938

Figures 12 e, f

Pseudochama clarionensis Willett 1938:48, pl. 4, figs. 1, 2 (Type locality: Off Clarion Island, Mexico, 18°22′N. Holotype LACM 1058, Paratype LACM 1058a); Keen 1971:151, fig. 354.

Shell exterior bright red, with scattered white, short, imbricated spines. The inner margin is delicately crenated. Interior white, clouded or streaked with bright rosy red.

Discussion: The short, white spines arising from the red exterior and the rich pinkish streaking of the interior distinguishes this elegant small species from all others. It is rarely collected and appeared endemic to Clarion Island until a specimen was collected in the Galapagos Islands (Keen 1971).

The species is generally cemented to small pebbles, or exists as colonies in fissures and on the underside of boulders in 27 to 55 meters. The northward range is Clarion Island, Mexico (18°22′N), extending southwards on the mainland coast to Isla del Tigre, Honduras (13°16′N). It is a frequent component of the rocky substrate epifauna of Barrington Island, Galapagos Group (0°51′S), but does not occur so far south on the mainland coast.

Pseudochama corrugata (Broderip 1835)

Figures 7 g, h

Chama corrugata Broderip 1835a:150 (Type locality: Corinto, Nicaragua, 12°29′N. Paratype BM(NH) 1950.11.1.23); Broderip 1835b:305, pl. 38, fig. 7; Reeve 1847: pl. 2, fig. 9; Clessin 1889:37, pl. 16, fig. 2; Lamy 1910:88.

Pseudochama corrugata (Broderip), Olsson 1961:226, pl. 34, fig. 4-4d; Keen 1971:151, fig. 355.

Shell highly variable, sculpture generally obscure, sometimes with broad foliations, exterior radially grooved, often with brown lines. Interior with extensive purple staining.

Discussion: This is the largest of western American *Pseudochama* and is easily recognized by the extensive purple staining of the shell interior. It is the commonest off the northern Peruvian coast, more rarely occurring off Panama, and sporadically to the Gulf of California, Mexico. It is a warm water species and does not extend into the cool water south of Point Aguja, Peru. The geographic range is from Sechura Bay, Peru (5°40′S), to Isla Partida, Mexico (28°52′N). *P. corrugata* is generally cemented to rock in exposed locations, more rarely on dead bivalve shell, in the intertidal zone to 5 meters.

Pseudochama dalli new name

Figure 12 d

Chama inermis Dall (Carpenter MS) 1871:148 (Type locality: unknown: not Puget Sound, Washington. Holotype USNM 24108). Not *Chama imbricata inermis* Deshayes 1863.

Pseudochama inermis (Dall), Palmer 1963:307, pl. 61, fig. 8-10; Keen 1971:151, fig. 356.

Shell smooth, covered by a thin adherent brownish yellow periostracum. Free valve may bear a purple ray. Interior white, sometimes with a purple brown patch. Margin smooth.

Discussion: This rare species is readily identifiable by the lack of exterior processes and the thin shining periostracum. It may possibly be a teratological specimen of *P. panamensis* (Reeve) but until more material is available the taxon must be retained. The holotype was obtained supposedly from Puget Sound, by J. Rowell, who collected from California to Panama. This material was deposited in the Smithsonian Institution and examined by P. P. Carpenter, who correctly surmised that it was tropical and not from Puget Sound. Because of the doubtful type locality Carpenter did not release his manuscript name and description for this species. Dall published the name; however, it is preoccupied by Deshayes (1863) for a variety of *Chama imbricata* Broderip 1835 from the Indian Ocean. Pilsbry and Lowe (1934) illustrate a fine specimen collected in 1930 from the Tres Marias Islands off Mexico. The species occurs from Panama Bay, Panama (9°N) to Tres Marias Islands, Mexico (21°26′N) and has been collected only from wooden pilings at the subtidal level to 5 meters. The type location, Tres Marias Islands, Mexico (21°26′N) is here designated.

Pseudochama exogyra (Conrad 1837)

Figures 10 d-f

Chama exogyra Conrad, 1837:356 (Type locality: Santa Barbara, California, 34°23′N. Syntypes BM(NH) 1961.5.20.155); Reeve 1847: pl. 7, fig. 38; Tryon 1872:117; Clessin 1889:26, pl. 10, fig. 5; Lamy 1927:337.

Pseudochama exogyra (Conrad), Durham 1950:73, pl. 17, figs. 4, 13 (Pliocene to Recent of Mexico); Addicott 1964:146 (Pleistocene of California); Yonge 1967:49; Smith and Gordon 1948:173.

Pseudochama granti Strong 1934:137, pl. 8, figs. 6, 7 (Type locality: Clarion Island, Mexico, 18°N. Holotype CAS 5808); Smith and Gordon 1948:137; Dibblee 1966:58 (Pleistocene of California).

Shell white, sometimes splashed with red, more rarely with green. Sculpture of concentric lamellae that may be produced into broad spines. Interior white, inner margin smooth; commissural shelf may be wide.

Discussion: This most northerly representative of *Pseudochama* may be difficult to recognize due to excessive abrasion and obliteration of the surface detail, but the plain shell margins and translucency of the exterior surface made it unlikely to be confused with other species. I consider *P. granti* Strong the subtidal form in which the sculpture tends to be smaller and more regular, less likely to be eroded. The type variant of *P. exogyra* is intertidal or just subtidal, and is distributed from central Oregon (approximately 44°N), to San Diego, California (32°40′N). *P. granti* occurs from 20 to 155 meters and extends from the southern British Columbia border (48°N) to San Benito Island, Mexico (28°N). In 1962 I collected a single specimen in 155 meters off the west coast of the Queen Charlotte Islands (53°N). Clarke and Clarke (1974) reported a single specimen of *P. exogyra* from a Nootka Indian shell midden on the west coast of Vancouver Island, British Columbia (49°35′N). A number of other molluscan species have been collected from time to time far from their normal range. These chance occurrences cannot be considered part of the normal distribution pattern as the errant specimens do not constitute established, breeding populations.

Odhner (1919) considered *P. exogyra* to be identical to *echama rotunda* Clessin, 1889 from the Gulf of Mexico. I do not agree with his conclusion.

Pseudochama janus (Reeve 1847)

Figure 11 a, b

Chama imbricata var α Broderip 1835a:149 (Type locality: Galapagos Islands. Syntypes BM(NH) 1950.11.1.36-38); Broderip 1835b:304, pl. 39, fig. 3; Soot-Ryen 1931:314.

Chama janus Reeve 1847: pl. 7, sp. 36 (Type locality: Galapagos Islands. Syntypes BM(NH) 1950.11.1.36-38); Clessin 1889:43, pl. 17, fig. 6; Lamy 1927:340.

Pseudochama janus (Reeve), Keen 1971:151, fig. 357.

Exterior with a uniform elegant brown striping. Upper valve medially bisected into two distinct surface patterns of ornamentation, the posterior section with brown lines and a few short scales. Interior white, margins crenulated only on dorsal posterior portion.

Discussion: The medial bisection of the free valve into two distinct pattern zones readily distinguishes this species from all other west American chamids.

There is no doubt that material from different locations was included by Broderip when he proposed *C. imbricata*. The nominate species is a common Indo-Pacific chamid, while var α is Galapagan and Reeve was correct in suggesting a new name. Odhner (1919) considered *P. janus* synonymous with *P. corrugata* (Broderip 1835), a totally unwarranted conclusion. The species appears endemic to the Galapagos Islands, cemented to molluscan shells in 10 to 25 meters. Osorio and Bahamonde (1970) record *C. imbricata* Broderip 1835 from the Juan Fernandez Islands (33°S), and the literature contains records of *P. janus* from Mexico. I have been unable to confirm these records and consider them probably due to misidentification of *P. panamensis* (Reeve 1847).

Pseudochama panamensis (Reeve 1847)

Figures 12 a-c

Chama panamensis Reeve 1847: pl. 8, sp. 45 (Type locality: Panama. Holotype (BM(NH) 1950.11.1.23); Clessin 1889:32, pl. 13, fig. 5; Lamy 1927:330.

Pseudochama panamensis (Reeve), Olsson 1961:225, pl. 33, fig. 1-1b; Keen 1971:151, fig. 358.

Shell generally dorsoventrally prolonged. Exterior white, with delicate lines of brown. Attached valve with a few hyote spines. Free valve with concentric rows of wide longitudinally ribbed imbricated spines and a small area of the dorsal posterior portion with concentric scales. Interior white, sometimes with patches of brown or yellow, shell margins smooth. Attachment area extensive.

Discussion: This species, though with a wide range, is of sporadic occurrence. The ribbed imbricated spines of the upper valve and small zone of concentric lamellae (''two-fold structure'' of Reeve) easily distinguish it from other chamids. However, specimens with poor sculpture and heavy brown striping may be mistaken for *P. janus* (Reeve). This species appears limited to clefts and fissures in massive rocks from the middle tidal level to 10 meters. The range is from Gonzaga Bay, Gulf of California, Mexico (29°50′N) to Cape San Francisco, Ecuador (0°40′N). The original type locality ''Panama'' is vague, so Punta Garachina, Panama (8°07′N, 78°39′W) is here designated the type locality.

Pseudochama saavedrai Hertlein and Strong 1946

Figures 8 d-f

Pseudochama saavedrai Hertlein and Strong 1946:110, pl. 1, figs. 1, 3, 8, 10. (Type locality: Manzanillo, Mexico, 19°00′N, in 45 meters. Holotype CAS 9189A.); Hertlein 1957:63 (Pleistocene of Mexico); Keen 1971:151, fig. 359.

Shell white to light yellow. Lower valve with concentric appressed lamellae. Upper valve ornamented with concentric longitudinally striated lamellae, prolonged into two radial rows of wide imbricated spines. Interior white, margins coarsely crenulated, comissural shelf wide. Attachment area small.

Discussion: The species is readily distinguished by the overlapping lamellae produced into two radial rows of spines. The holotype is a poor specimen and does not do justice to the beauty of this species. Material from Panama in the Allan Hancock Foundation holdings and other collections is more solid than Mexican representatives and the lamellae are shorter and coarser but it is undoubtedly this species.

P. saavedrai is frequently attached to dead shells in regions of small cobbles and rock fragments in the low intertidal to 55 meters. In ranges from Puerto Penasco, Gulf of California, Mexico (31°20′N) to Chacahua Bay, Mexico (15°55′N) and the Allan Hancock Foundation has material from Secas Island, Panama (7°58′N).

ACKNOWLEDGMENTS

My sincere appreciation is due to J. S. Garth, Senior Curator (now Professor Emeritus) of the Allan Hancock Foundation, for placing the chamid collection in my hands. As this material largely consists of detached, often juvenile, valves unsuitable for illustration, I am indebted to fellow workers, notably S. S. Berry, C. Angermeyer, and the late W. J. Eyerdam, who donated specimens that are now on deposit in the Los Angeles County Museum of Natural History. I am also indebted to K. M. Way of the British Museum (Natural History) for furnishing biographical details of certain nineteenth century collectors and to J. Rosewater of the United States National Museum for the loan of type material. I am grateful to E. V. Coan, A. M. Keen and J. H. McLean for generous advice and constructive criticism.

RESUMEN

Diecinueve especies de Chamidae viven en el Pacífico Oriental Americano y predominan en aguas templadas poco profundas. Las amplias colecciones de la Fundación Allan Hancock de la universidad del Sur de California proporcionan las bases para esta revisión sistemática y distributiva. Se concluye que se ha determinado genéticameente la valva de u ión. Se presenta una nueva interpretación de la ontogénesis principal. Se propone el nombre *Pseudochama dalli* para un nombre ya asignado. También se proponen tres nuevas especies *Chama arcana, C. garthi* y *C. tinctoria.*

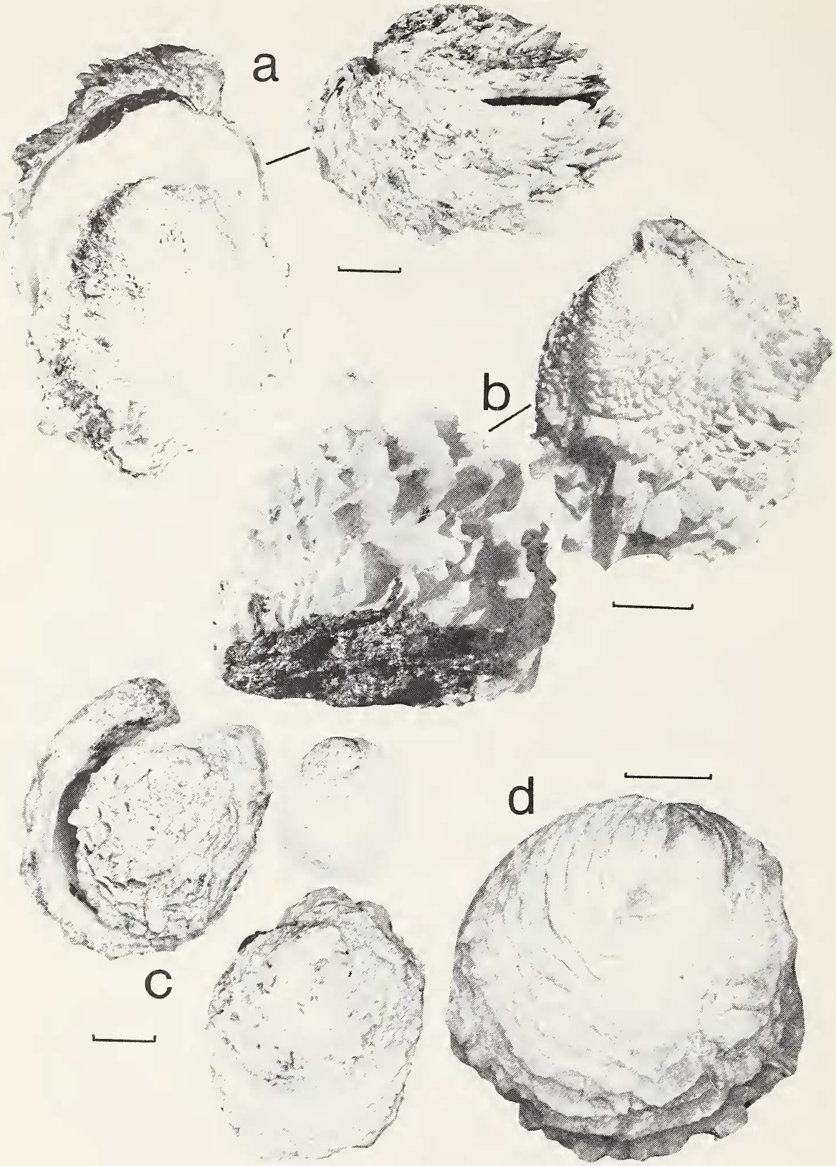

FIGURE 4. (a) *Chama arcana* new species, Newport Bay, California, holotype, LACM 1723; (b) *Chama arcana* new species, Monterey, California, LACM A8881.1; (c) *Chama pellucida Broderip, Iquique, Chile, topotypes, LACM A8881.2; (d) Chama chilensis* Philippi (= *C. pellucida*), Pliocene, Laguna de Cahuil, Chile, holotype, MNHN no number. Scale = 1 cm.

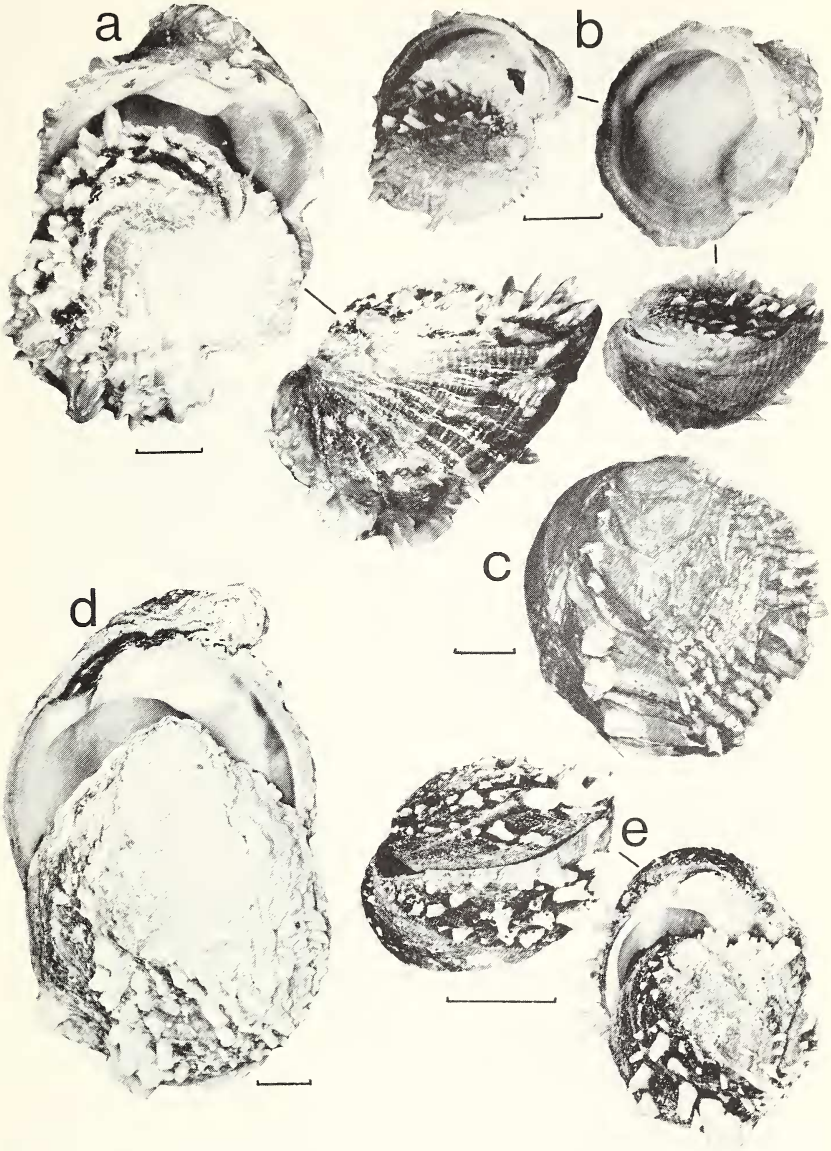

FIGURE 5. (a) *Chama tinctoria* new species, Bahia Honda, Panama, holotype, AHF 169; (b) *Chama tinctoria* new species, Bahia Honda, Panama, paratype, AHF 170; (c) *Chama tinctoria* new species, Panama Bay, Panama, MNHN no number; (d) *Chama buddiana* C. B. Adams, Isla del Rey, Panama Bay, Panama, LACM A8881.3; (e) *Chama buddiana* C. B. Adams, Albemarle Island, Galapagos Islands, Ecuador, LACM A8881.4. Scale = 1 cm.

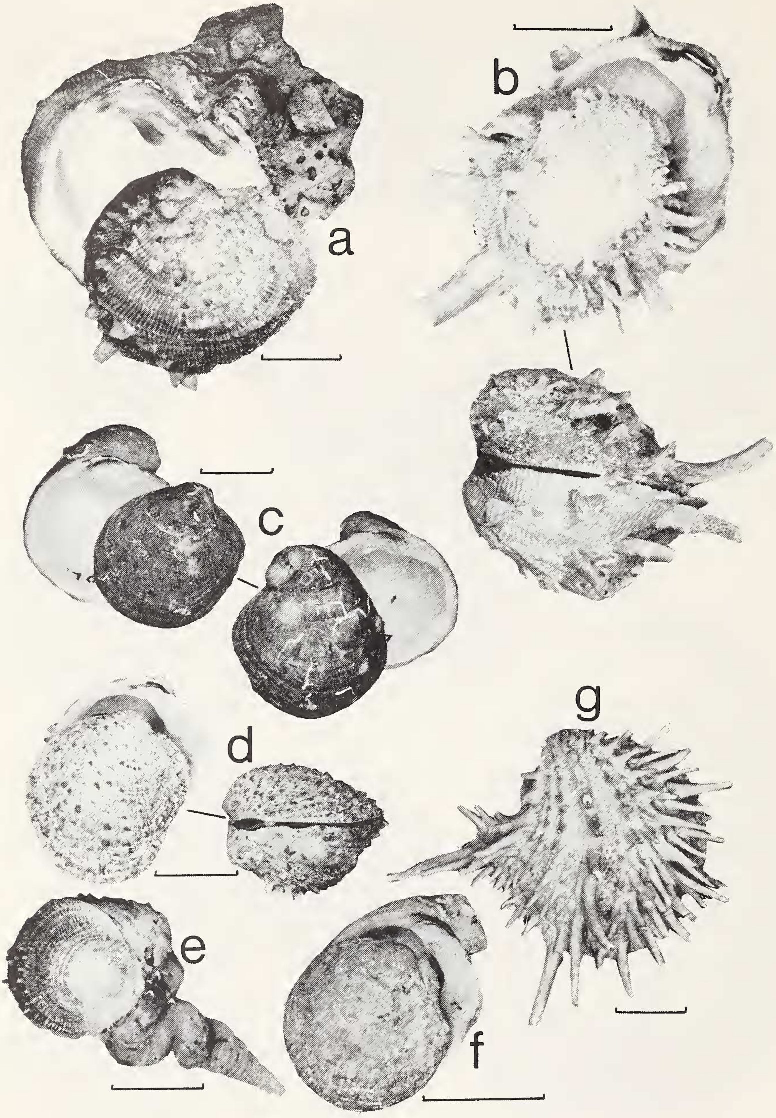

FIGURE 6. (a) *Chama sordida* Broderip, Isle of Cuna, Central America, syntype, BM(NH) 1950.11.1.52; (b) *Chama sordida* Broderip, Gorgona Island, Colombia, AHF 1262; (c) *Chama corallina* Olsson, Punta Escondido, Panama, holotype, USNM 701157; (d) *Chama corallina* Olsson, Isla Cinche, Bahia Honda, Panama, LACM A881.5; (e) *Chama corallina* Olsson, Gulf of California, Mexico, Mrs. E. E. Wahrenbrock; (f) *Chama corallina* Olsson, Punta Escondido, Panama, topotype, AHF 1264; (g) *Arcinella californica* (Dall), Cedros Island, Mexico, holotype, USNM 96252. Scale = 1 cm.

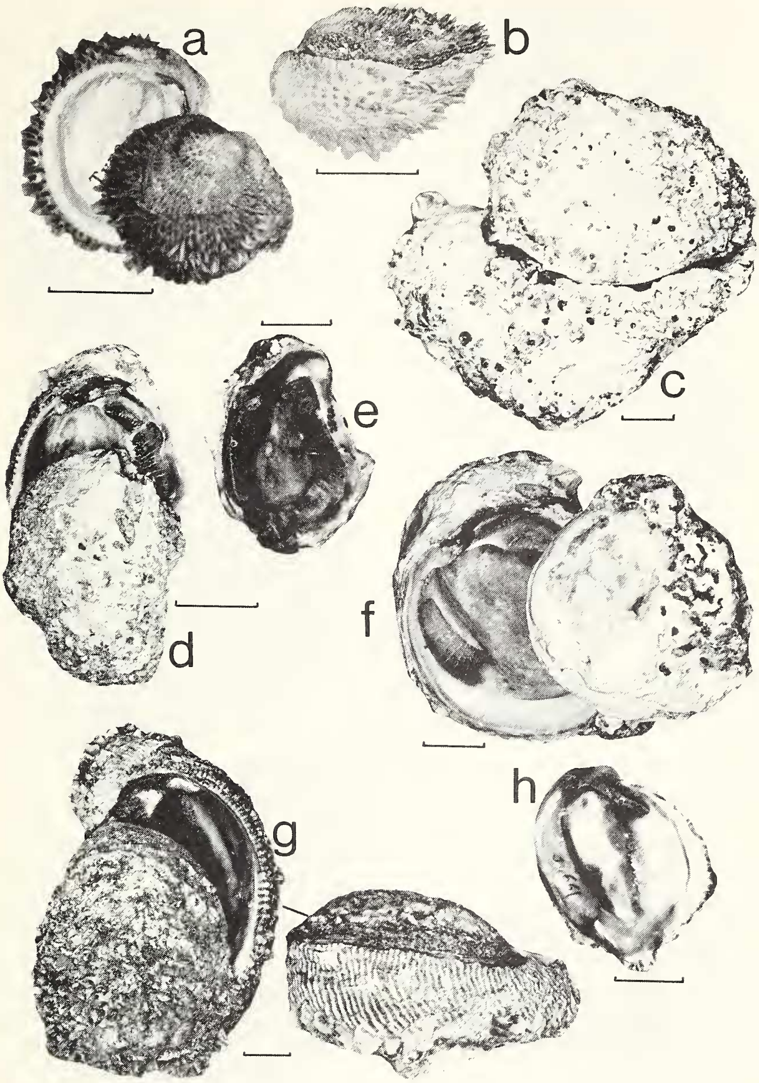

FIGURE 7. (a) *Chama echinata* Broderip, Puerto Portrero, Ecuador, syntype, BM(NH) 1950.11.1.21; (b) *Chama echinata* Broderip, Banderas Bay, Mexico, LACM A8881.6; (c) *Chama echinata* Broderip, Isla Bona, Gulf of Panama, Panama, LACM A8881.7; (d) *Chama echinata* Broderip, Banderas Bay, Nayarit, Mexico, LACM A8881.19; (e) *Chama echinata* Broderip, Cedros Island, Mexico, LACM A8881.8; (f) *Chama coralloides* Reeve (= *C. echinata*), Puerto Portrero, Ecuador, holotype, BM(NH) no number; (g) *Pseudochama corrugata* (Broderip), Tumbez, Peru, CAS 36666; (h) *Pseudochama corrugata* (Broderip), Caleto Mero, Peru, CAS 36661. Scale = 1 cm.

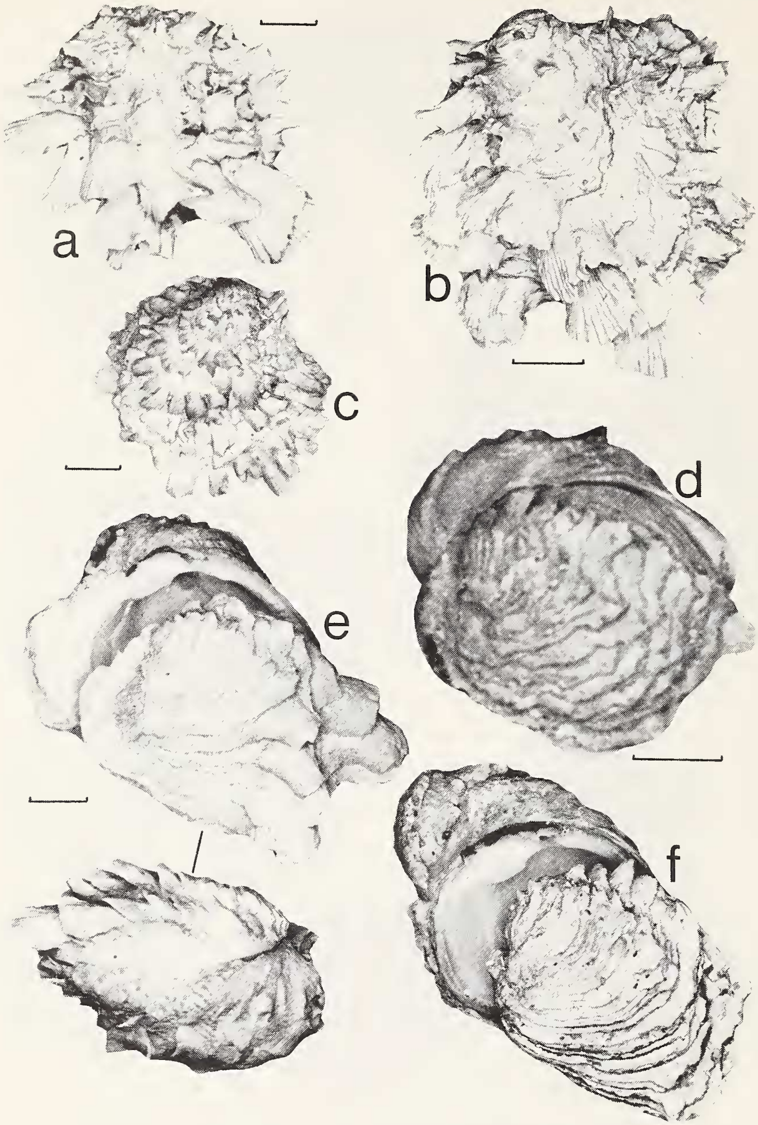

FIGURE 8. (a) *Chama frondosa* Broderip, Isla La Plata, Ecuador, holotype, BM(NH) 1950. 11.1.55; (b) *Chama frondosa* Broderip, Isla La Plata, Ecuador, paratype, BM(NH) 1950. 11.1.54; (c) *Chama parasitica* Rochebrune (= *C. frondosa*), San Jose Island, Mexico, holotype, MNHN no number; (d) *Pseudochama saavedrai* Hertlein and Strong, Manzanillo, Mexico, holotype, CAS 9189A; (e) *Pseudochama saavedrai* Hertlein and Strong, Manzanillo, Mexico, topotype, LACM A5498; (f) *Pseudochama saavedrai* Hertlein and Strong, Secas Island, Panama. LACM A8881.9. Scale = 1 cm.

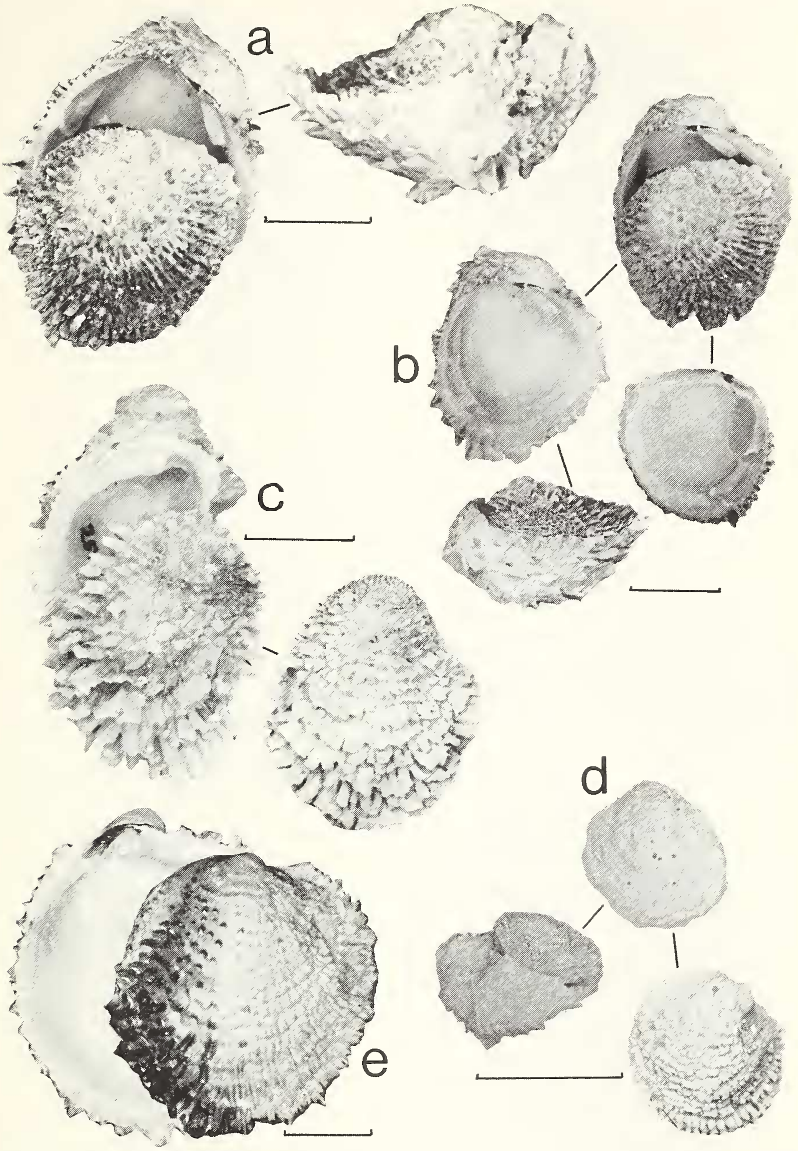

FIGURE 9. (a) *Chama garthi* new species, Octavia Bay, Colombia, holotype, AHF 167; (b) *Chama garthi* new species, Octavia Bay, Colombia, paratype, AHF 168; (c) *Chama squamuligera* Pilsbry and Lowe, Santa Cruz Island, Galapagos Islands, Ecuador, LACM A8881.10; (d) *Chama squamuligera* Pilsbry and Lowe, Barrington Island, Galapagos Islands, Ecuador, LACM A8881.11; (e) *Chama spinosa* Broderip, South Marutea (extralimital), holotype, BM(NH) no number. Scale = 1 cm.

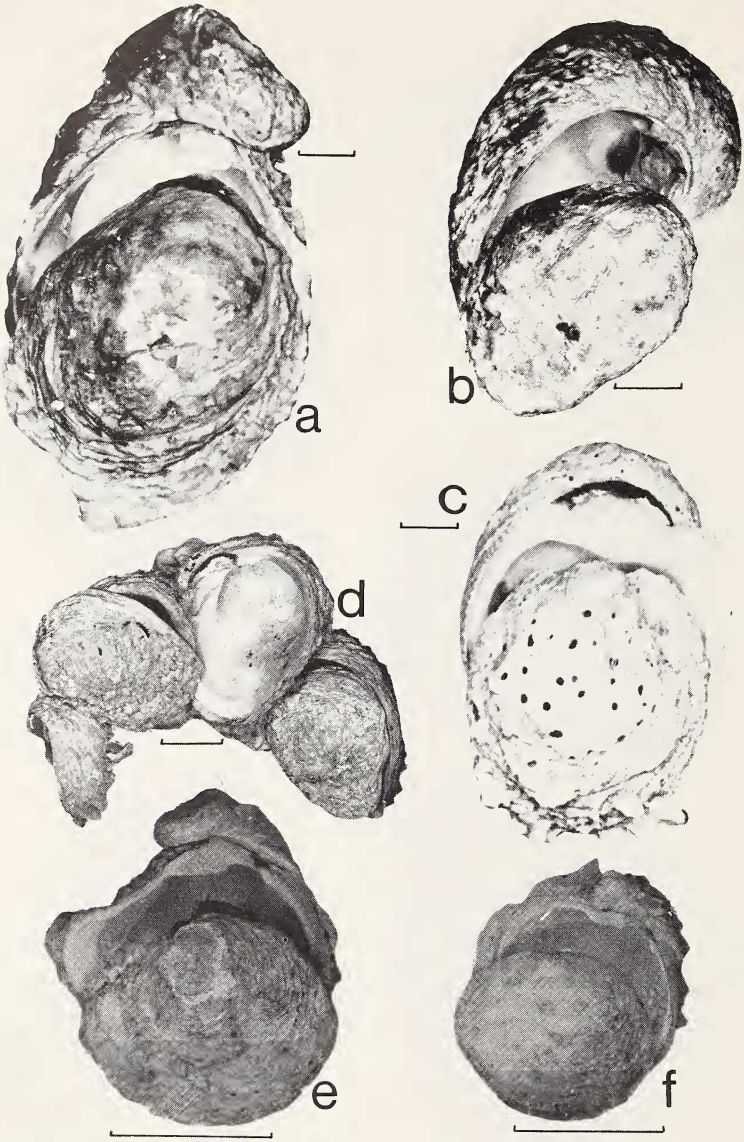

FIGURE 10. (a) *Chama producta* Broderip (= *C. mexicana*), Gulf of Tehuantepec, Mexico, holotype, BM(NH) 1950.11.1.60; (b) *Chama frondosa fornicata* Carpenter (= *C. mexicana*), Mazatlan, Mexico, syntype, BM(NH) Carpenter Collection 440; (c) *Chama mexicana* Carpenter, Bahia Concepcion, Baja California, Mexico, LACM A8881.12; (d) *Pseudochama exogyra* (Conrad), Santa Barbara, California, syntypes, BM(NH) 1961.5.20.155; (e) *Pseudochama exogyra* (Conrad), Vancouver Island, British Columbia, Canada, LACM A8881.13; (f) *Pseudochama exogyra* (Conrad), Catalina Island, California, LACM A8881.14; Scale = 1 cm.

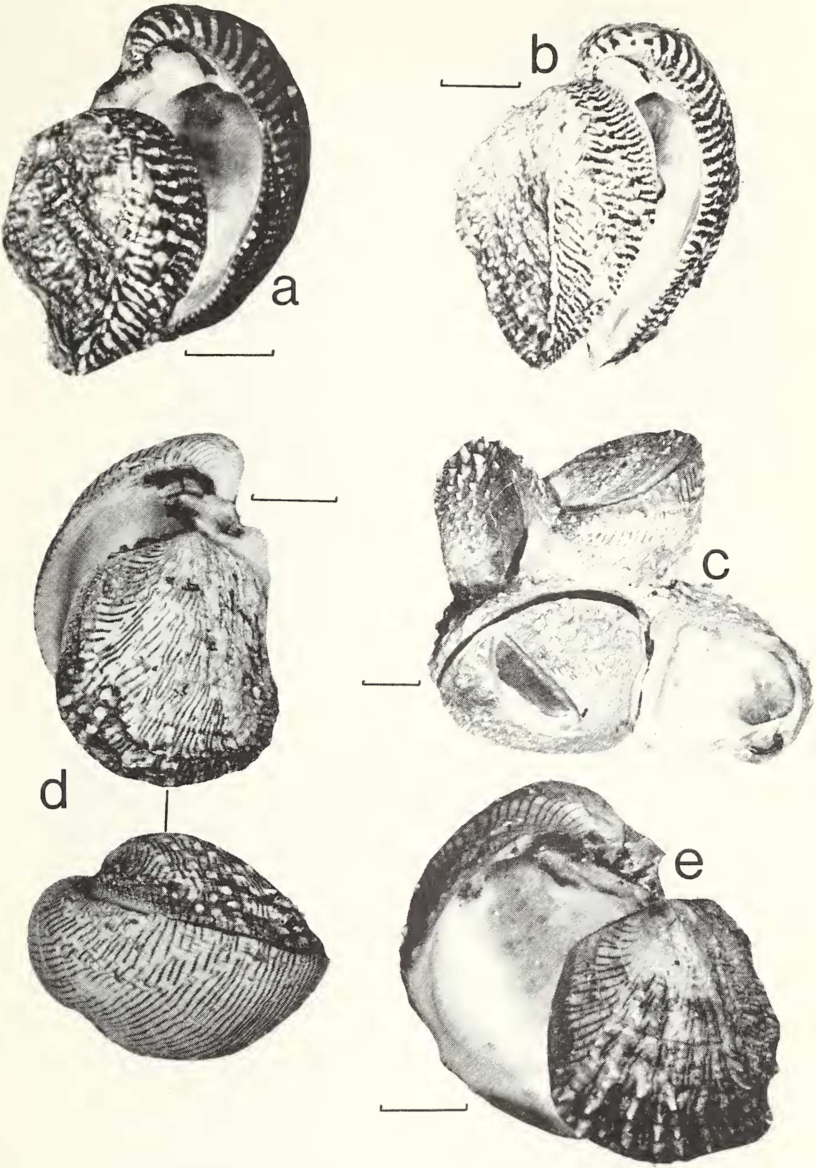

FIGURE 11. (a) *Pseudochama janus* (Reeve), Galapagos Islands, Ecuador, holotype, BM(NH) 1950.11.1.36; (b) *Pseudochama janus* (Reeve), Albemarle Island, Galapagos Islands, Ecuador, LACM A8881.15; (c) *Chama digueti* Rochebrune (= *C. venosa*), San Jose Island, Mexico, syntypes, MNHN no number; (d) *Chama venosa* Reeve, Guaymas, Gulf of California, Mexico, BM(NH) no number; (e) *Chama venosa* Reeve, locality unknown, holotype, BM(NH) 1950.11.1.4. Scale = 1 cm.

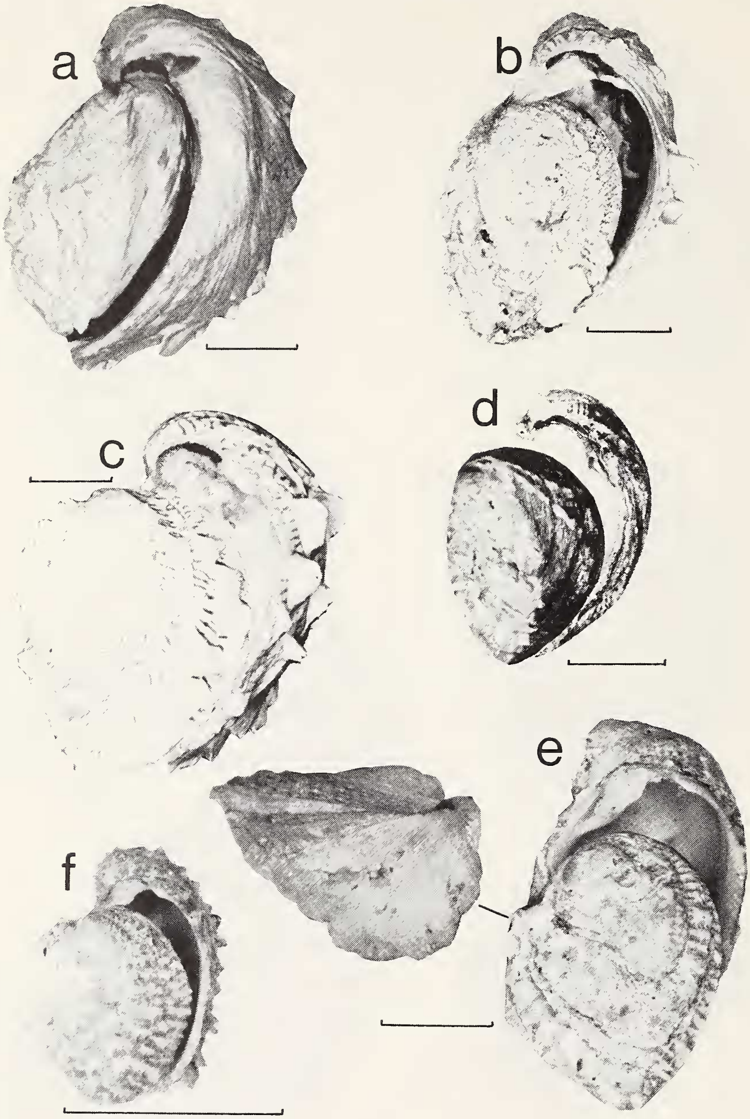

FIGURE 12. (a) *Pseudochama panamensis* (Reeve), Panama, holotype, BM(NH) 1950.11.1.23; (b) *Pseudochama panamensis* (Reeve), Bahia Gonzaga, Gulf of California, Mexico, LACM A8881.16; (c) *Pseudochama panamensis* (Reeve), La Paz, Baja California, Mexico, MNHN no number; (d) *Pseudochama dalli* new name (= *C. inermis*), Panama Bay, Panama, BM(NH) no number; (e) *Pseudochama clarionensis* Willett, Barrington Island, Galapagos Islands, Ecuador, LACM A8881.17; (f) *Pseudochama clarionensis* Willett, Clarion Island, Mexico, LACM A8881.18. Scale = 1 cm.

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